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RESPONSE OF *CAREX*-DOMINATED WETLANDS TO ALTERED TEMPERATURE AND FLOODING PATTERNS

Wisconsin Power Plant Impact Study

by

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This report presents the 1974 to 1977 results of a study undertaken on the site of the Columbia Electric Generating Station to determine the effects of leakage from the cooling lake on wetland vegetation. Results showed that changes in water levels and water temperatures caused by seepage from the cooling lake led to significant changes in wetland plant populations and communities within 1 yr after the Columbia Station began operation. Dominant perennial rhizomatous species of *Carex* decreased in density and distribution, hydrophytic species increased, and annual species increased markedly. A predominant trend of decreasing species diversity and richness was observed from 1974 to 1977. However, no uniform relationship was observed between diversity and intensity of disturbance--neither species richness nor distribution of their abundances.

Recommendations for future research are made with respect to the development of effective management and assessment tools for wetland plant communities.

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FOREWORD

The U.S. Environmental Protection Agency was established as a focus of scientific, governmental, and public efforts to improve the quality of the environment. These efforts require expansion of our understanding of the mechanisms that govern environmental changes and in particular those changes that result from our own manipulations of the environment. One specific thrust of these efforts must be the continuous development of more effective and more efficient methods for analyzing the environment and the changes occurring in it.

One such project, which the Environmental Protection Agency is supporting through its Environmental Research Laboratory in Duluth, Minnesota, is the study "The Impacts of Coal-Fired Power Plants on the Environment." The Columbia Generating Station, a coal-fired power plant near Portage, Wis., has been the focus of all field observations. This interdisciplinary study, involving investigators and experiments from many academic departments at the University of Wisconsin, is being carried out by the Water Resources Center and Institute for Environmental Studies at the University of Wisconsin-Madison. Several utilities and state agencies are cooperating in the study: Wisconsin Power and Light Company, Madison Gas and Electric Company, Wisconsin Public Service Corporation, Wisconsin Public Service Commission, and Wisconsin Department of Natural Resources.

The results of a study undertaken to determine the effects of leakage from the cooling pond on wetland vegetation are presented in this report. The study included field inventory and classification of plant communities, vegetation monitoring, field and laboratory experiments to test hypotheses regarding mechanisms controlling population changes, and assessment of field and theoretical approaches. Results showed that changes in water levels and water temperatures caused by seepage from the cooling pond led to significant changes in wetland plant populations and communities within 1 yr after the power plant began operating.

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ABSTRACT

This report presents the 1974 to 1977 results of a study undertaken on the site of the Columbia Electric Generating Station to determine the effects of leakage from the cooling lake on wetland vegetation. The study included four phases: Field inventory and classification of plant communities; vegetation monitoring; field and laboratory experiments to test hypotheses regarding mechanisms controlling population changes; assessment of field and theoretical approaches. Results showed that changes in water levels and water temperatures caused by seepage from the cooling lake led to significant changes in wetland plant populations and communities within 1 yr after the Columbia Station began operation. In general, dominant perennial rhizomatous species of *Carex* decreased in density and distribution, hydrophytic species such as *Typha latifolia* increased, and annual species such as *Bidens cernua* and *Pilea pumila*, which had been insignificant or absent before disturbance, increased markedly. Major shifts in dominance and diversity patterns and a continuing trend of decreasing vegetative cover occurred from 1974 to 1977. Open water and exposed mudflats replaced the previously closed and densely vegetated perennial plant communities over an increasing portion of the study area. Annuals colonized some of the habitat opened by the removal of perennial species, but large areas remained unvegetated. By 1977, 19% of the quadrats sampled in the area of major impact had no rooted vegetation. Another 2% contained only annual vegetation.

A predominant trend of decreasing species diversity and richness was observed from 1974 to 1977. However, no uniform relationship was observed between diversity and intensity of disturbance--neither species richness nor distribution of their abundances. Disturbance did not simply increase or decrease diversity. Species richness, diversity, and equitability sometimes varied independently. All of the diversity measures used decreased in most cases, but increased in others, and frequently did both during the period from 1974 to 1977 as the spatial distribution and intensity of disturbance increased on the Columbia site. Caution is urged in interpreting diversity data for wetlands, subject to human-induced alterations in the physical environment.

Physiological and phenological data from laboratory and field experiments related the response of *T. latifolia* and *C. lacustris* to altered seasonal patterns of carbohydrate storage and shoot phenology induced primarily by groundwater temperatures out of phase with normal cycles of plant growth. Results for *C. lacustris* and *T. latifolia* suggested that the likelihood of predicting the response of dominant species to disturbance would be enhanced by knowing the key characteristics of their life cycle. The extreme sensitivity of *C. lacustris* appeared to be a consequence of its particular life history cycle and the timing, as well as the magnitude, of the disturbance.

Recommendations for future research are made with respect to the development of effective management and assessment tools for wetland plant communities.

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SECTION 1

INTRODUCTION

SCOPE OF STUDY

Research on wetland plant responses was--like other studies--carried out at the Columbia Electric Generating Station site, conducted as part of a larger program designed to evaluate environmental changes brought about by construction and operation of the 1100 MW facility. The research objectives of the program as a whole were formulated in 1970 in the context of Wisconsin's recent Shoreline Zoning Act (1965), imminent passage of the Wisconsin Environmental Policy Act (1971), and a long history of protection of navigable waters under the Public Trust Doctrine of the State Constitution. Regulatory responsibilities established under these legislative and constitutional mandates required evaluations, in advance, of the prospective effects of the proposed development. The Columbia study, undertaken initially with support from the three Wisconsin utilities building the power plant (Wisconsin Power and Light Co., Madison Gas and Electric Co., and the Wisconsin Public Service Corp.), was intended to provide information for government and industry in future environmental protection decisions involving coal-fired steam electric plants. Additional support provided by the U.S. Environmental Protection Agency (U.S. EPA) permitted the study to expand between 1975 and the present to take advantage of the baseline studies and obtain more definitive answers to a wide range of questions on environmental effects.

The project was a unique opportunity to examine fundamental ecological questions about the response of wetland ecosystems to the external influences of nearby development. The Columbia station and its associated facilities which were under construction in 1971 at the time the study was initiated, were located adjacent to and in the floodplain of the Wisconsin River. Most (81.9%) of the 1900-ha site in its pre-construction state was wetland (Figure 1). Almost 50% of the site was an extensive marsh--sedge meadow (31%) or emergent aquatic vegetation (17%)--considered to be important as walleye and northern pike spawning habitats. These areas represented a major portion of the nonwooded wetlands remaining on the Wisconsin River in Columbia County.

The 200-ha cooling lake built for the generating station was sited in the marsh. The utilities and the project research staff predicted that the lake would leak substantial amounts of warm water. Although the effect of the leakage on the remaining marsh was not examined fully during pre-construction evaluation, it became a major question during later assessment of environmental effects from the Columbia power station development.

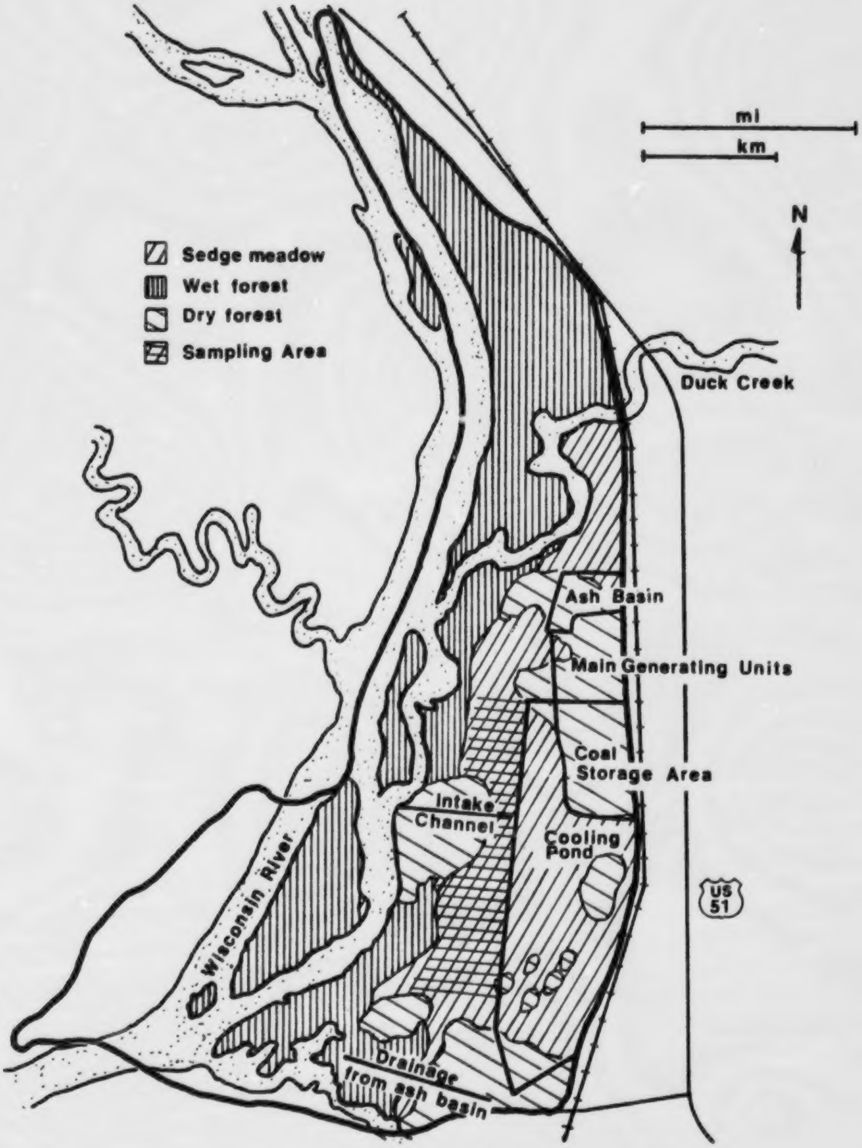
mi
km
N
Sedge meadow
Wet forest
Dry forest
Sampling Area
Duck Creek
Ash Basin
Main Generating Units
Coal Storage Area
Intake Channel
Cooling Pond
US 51
Wisconsin River
Drainage from ash basin

Figure 1. Plant communities at the Columbia Station prior to construction.

The wetland plant ecology study in the Columbia project was undertaken in 1974 to monitor vegetation changes associated with leakage from the cooling lake. Although it was known that the remaining wetlands would be affected by elevated groundwater levels and temperature increases due to leakage from the cooling lake, uncertainty existed regarding the nature and probable timing of the changes. Neither the type, magnitude, nor rate of change was predictable at the time. Using the existing paradigms for ecosystem response, potential effects considered by the 1973 Wisconsin Department of Natural Resources (WDNR) Environmental Impact Statement ranged from gradual decrease of intolerant species, increase of early-blooming plants, and decreased diversity to disrupted competitive interactions, changed rates of succession, and shifts to vegetation types--e.g., cattail--unsuitable for spawning habitat. In response to concern by the U.S. EPA, the National Marine Fisheries Service, the Bureau of Sport Fisheries and Wildlife, and the WDNR about effects on the marsh, the Army Corps of Engineers predicted no significant effect on the marsh vegetation, and the environmental assessment was left in that form (Department of the Army, St. Paul District Corps of Engineers 1974).

RESEARCH OBJECTIVES

The principal objective of the wetland vegetation study was to determine how the wetland plant communities west of the cooling lake (Figure 1) might change in response to mild heat and water stress which required answers to five basic questions:

1. What types of change would occur? Would changes occur at the level of species responses only, or would the marsh community change in unique ways? Would the composition or structure of the vegetation change?

2. What would be the magnitude of change? Would changes be within the range of natural variability in wetland ecosystems? How large an area would be affected?

3. At what rate would changes occur? Would the changes be gradual, or would they occur over a short time-frame and be more noticeable to observers?

4. Would a new equilibrium community become established or might the vegetation continue to change almost as long as the stress was continued?

5. Would changes be irreversible or might the communities recover following a period of complete abatement?

Wetland vegetation is dynamic, and methods for determining vegetation response to waste heat and elevated groundwater levels are not widely agreed upon. Wetlands in the upper midwest sometimes undergo natural shifts in species composition and structure without being subject to anthropogenic environmental influences (Bedford et al. 1974, Van der Valk and Davis 1978, Weller and Fredrickson 1974). Thus, the study had to examine whether changes induced by cooling lake leakage could be detected in the limits of existing field monitoring techniques. Furthermore, it was necessary to determine whether the theoretical pardigms for analysis provided criteria by which significant impact could be recognized.

The principal research objectives had to go beyond documenting resultant changes in wetland plant communities to an understanding of the process of change itself. The research goals designed to address the above questions, therefore, were aggregated into three broad categories:

1. Documenting the response of wetland plant species and communities to mild heat and water stress.

2. Determining causal mechanisms potentially relating vegetation changes to environmental variables that--in turn--could be related to leakage from the cooling lake.

3. Examining available field techniques and paradigms for recognizing, monitoring, and--if possible--projecting the probable effects of waste heat and elevated water levels on wetland vegetation.

These objectives--in summary--represent a program designed to document the change, establish the cause, and--in the process--improve assessment capabilities and theoretical understanding of the responses of freshwater wetland plant communities when placed under stress

At the same time, the wetland plant ecology study was undertaken in close cooperation with related research. Concerns with efficient assessment techniques, and the relative difficulty of wetland field work, led to the development of a separate subproject in the Columbia study to explore the integrated use of ecological and remote sensing methods in freshwater wetlands.

The wetland plant ecology research included four phases, namely, field inventory and classification of plant communities, vegetation monitoring, field and laboratory experiments to test hypotheses regarding mechanmisms regulating population changes, and assessment of field and theoretical approaches. Field surveys, species lists, and air photographs were used in the initital phases of the study to inventory, classify, and map the plant communities of the site. Phytosociological methods have been used since 1974 to monitor plant population changes and species composition. Field and laboratory experiments began in 1977, following intensive field studies during 1976. Measurements were made of changes in plant phenology and associated changes in amounts of carbohydrates stored in underground organs of two species of perennial plants. These measurements were used both to test hypotheses regarding mechanisms controlling population responses and to identify ecologically-based criteria by which significant impact on the wetland plant communities could be recognized and monitored in the field at the species level.

STUDY SITE

The study was conducted in non-forested freshwater wetlands lying immediately west of the cooling lake of the Columbia Electric Generating Station. The station is located in southcentral Wisconsin 6.4 km (4 miles) south of Portage (43° 33' N, 89° 27' W) on a 1900-ha site which is almost entirely in the floodplain of the Wisconsin River. Prior to construction, an extensive and diverse wetland system covered ≈ 80% of 1100 ha on the site declared for utility purposes. Dominant vegetation types in the wetland system included marsh (emergent aquatics and southern sedge meadow), southern lowland forest, and lowland shrub communities (Curtis 1959, Wisconsin DNR 1973). In 1971, more than 50% of the area was classed as non-forested wetland: sedge meadow - 31% (340 ha), emergent aquatics - 17% (183 ha), and lowland shrub communities - 2% (22 ha) (Wisconsin DNR 1973). Approximately 200 ha of this were filled for the construction of dikes or flooded for the cooling lake of the generating station (Figure 2). The non-forested wetlands remaining west of the cooling lake, between it and the lowland forest bordering the Wisconsin River, were selected for study.

The Columbia station consists of two 527-MW coal-fired electric power generating units, a 200 ha cooling lake, 28 ha ashpit, 16 ha coal pile, and other associated facilities. Construction began in 1971. Pumping to fill the cooling lake first began 13 June 1974 and ceased on 17 July 1974. The lake was almost empty due to high leakage rates by 1 September 1974. Pumping resumed 4 November 1974 after the dikes were sealed with bentonite. By 2 January 1975 the lake was full. Operation of the first unit began in May 1975. The second unit did not begin operation until spring 1978 (Andrews and Anderson 1980).

Data collection for this study began in June 1974 and continues to the present. Some preliminary studies of wetland vegetation on the site were carried out from 1971 to 1973 by Samuelson (1972). Studies of the groundwater system and surface flows on the site began in 1972.

The wetlands on the Columbia site are located in a regional groundwater discharge area and occupy a former channel of the Wisconsin River. A layer of peat varying in thickness from 1 to 3 m overlies a thin layer of organic clay and silt underlain by alluvial sands with clay lenses. Bedrock composed of Upper Cambrian sandstones and Pre-Cambrian granites occur at a depth of 125 m below the surface (Andrews 1978b).

Prior to filling the cooling lake, groundwater discharge, precipitation, and floodwaters supplied water to the extensive wetland communities on the site. Precipitation was the most important source, providing ≈ 76 cm/yr. Groundwater inflow averaged ≈ 22 cm/yr. Floodwaters from the Wisconsin River and Duck Creek frequently inundated the site, usually in early spring. However, their residence time in the wetlands was short (< 3 days) due to the gentle slope of the area toward the Wisconsin River. Other surface water inflows were minor (Stephenson and Andrews 1976).

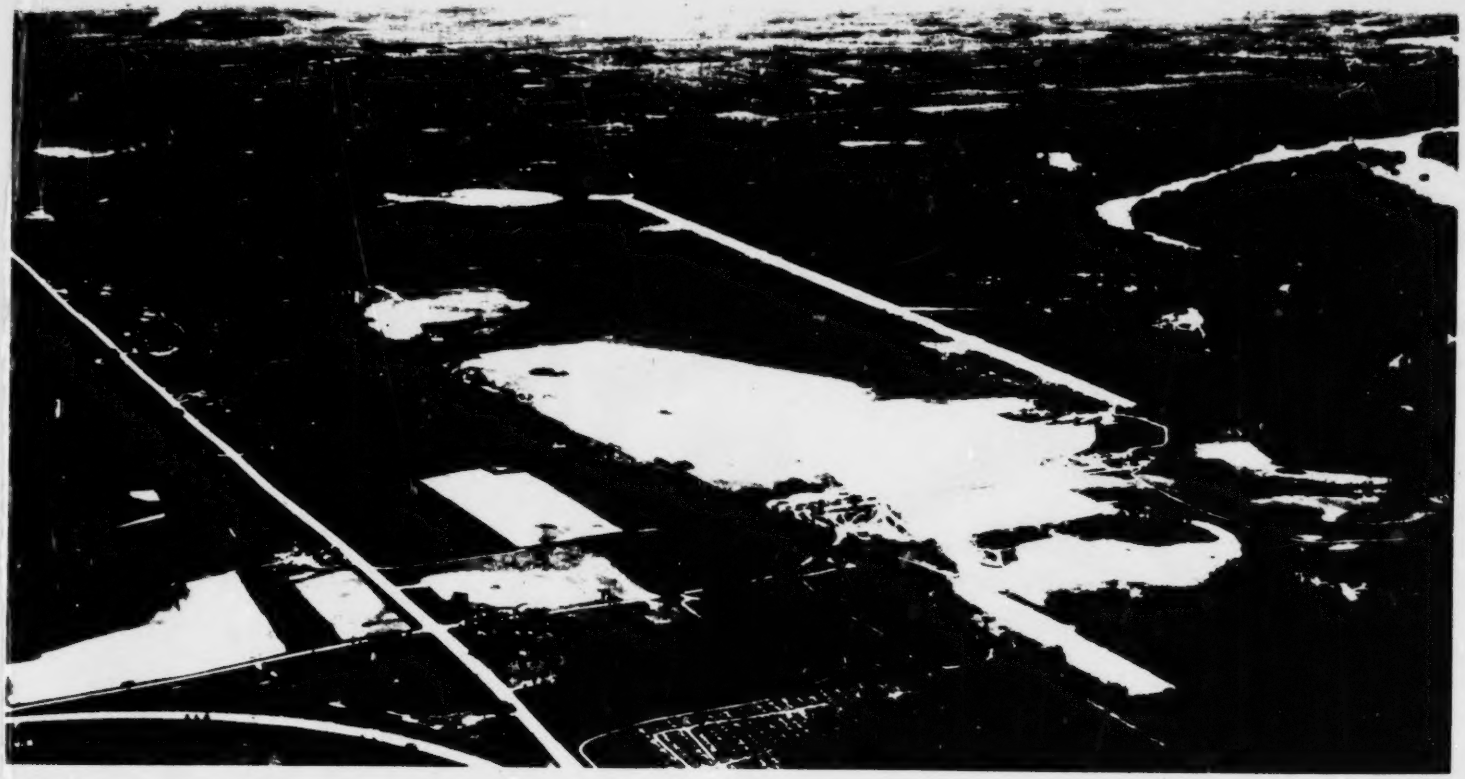

Figure 2. Aerial photograph of Columbia Station taken in 1971 showing area of meadow/marsh to be used for generating station, cooling pond, and dikes. Sampling area is above and immediately to the right of the dike shown intersecting the upper right-hand corner of the photograph.

Wetland surface water levels fluctuated widely prior to lake filling. Generally, levels were high during spring floods, decreased in summer, frequently to levels below the soil surface, and rose again in the fall as plant growth and evapotranspiration ceased (Stephenson and Andrews 1976).

The climate in the vicinity of the site is continental. Weather is seasonally variable with a large annual temperature range. Winters are cold and summers are warm. Mean annual temperature is 6.5°C (0.89 s.d.) with a mean summer maximum of 25.7°C (0.94 s.d.). Mean maximum temperature for winter is -3.3°C (1.78 s.d.) with a minimum mean of -12.9°C (2.06 s.d.) (Wang and Suomi 1958). The first killing frost is likely to occur around 30 September and the last around 1 May. Normal daily average monthly temperatures near Portage are: January, -7.78°C; May, 14.45°C; July, 22.78°C; and October, 9.45°C (Wang and Suomi 1957 and 1958). Average annual precipitation is $\sim$ 76 cm, with somewhat more than 50% of it falling between May and September.

SECTION 2

SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

SUMMARY

The environmental impact statement for the Columbia Electric Generating Station (Department of the Army, St. Paul District Corps of Engineers 1974) raised but did not answer the question of significant change occurring in wetland plant communities on the site as a result of leakage from the cooling lake. This report presents the results of a study undertaken on the site from 1974 to 1977 to determine the effects of leakage on wetland vegetation. The study included four phases: 1. Field inventory and classification of plant communities, 2. vegetation monitoring, 3. field and laboratory experiments to test hypotheses regarding mechanisms controlling population changes, and 4. assessment of field and theoretical approaches. Field surveys, species lists, and air photographs were used in the initial phases of the Columbia Study to inventory, classify, and map the plant communities of the site. Phytosociological methods have been used since 1974 to monitor changes in plant populations and community structure. Field and laboratory experiments began in 1977, following intensive field studies during 1976. Measurements were made of alterations in plant phenology and associated changes in amounts of non-structural carbohydrates stored in underground organs of two species of perennial plants. These measurements were used to test hypotheses regarding the causes of population decline and to identify ecologically based criteria by which significant impact on the wetland plant communities could be recognized and monitored in the field at the species level.

The scope of the study, research objectives, and description of the study site are summarized in Section 1. Results of the first two phases of the work covering changes in wetland plant populations and community structure are presented in Section 3. Section 4 reports the results of field and laboratory measurements of changes in plant phenology and patterns of carbohydrate storage. It identifies field signs of heat stress and suggests general species characteristics that may be useful indicators of potential sensitivity to stress. Initial assessment of field techniques and paradigms of analysis that might improve assessment capabilities and theoretical understanding of the responses of wetland vegetation to anthropogenic disturbance are discussed in Sections 3 and 4.

CONCLUSIONS

Results of data collected from 1974 to 1977 showed that changes in water levels and water temperature caused by seepage from the cooling lake led to significant changes in the plant populations and communities.

Plant population data showed that species were not equally sensitive to flooding, heat stress, or increased surface water flow. Some species, e.g., *Carex lacustris* and *C. rostrata*, were extremely sensitive, declining rapidly and dramatically in all communities. Other perennial species, e.g., *C. stricta* and *Calamagrostis canadensis*, responded more slowly, decreasing only after 1976. *Typha latifolia*, on the other hand, increased continuously in the EMERGENT community and invaded all other communities. Other hydrophytic but non-persistent species, e.g., *Sagittaria latifolia*, increased in some communities. *Lemna minor*, a floating annual, increased dramatically in expanding areas of open water. Annual species, e.g., *Bidens cernua* and *Pilea pumila*, which had been insignificant or absent before disturbance, increased markedly where perennial dominants declined.

Results of community level measure of wetland response to leakage from the Columbia cooling lake showed significant changes occurring in the structure of the plant communities. In addition to major shifts in dominance and diversity patterns in each plant community, a continuing trend of decreasing vegetative cover occurred in the Columbia wetlands from 1974 to 1977. Open water and exposed mudflats replaced the previously closed and densely vegetated perennial plant communities over an increasing portion of the study area. Annuals colonized some of the habitat opened by the removal of perennial species, but large areas remained unvegetated. By 1977, 19% of the quadrats sampled in the area of major impact had no rooted vegetation. Another 2% contained only annual vegetation.

The magnitude of effect produced at both the population and community levels appears to be outside the range of natural variability for this particular wetland. Shifts toward more hydrophytic species and decreasing vegetative cover are not uncommon for some wetland systems (Van der Valk and Davis 1976), but evidence for the Columbia site suggests that the 1974 vegetation represented a fairly long-lived community type under historically existing environmental conditions. The data from this study are limited since they contain only 1 yr of pre-impact measures. However, early surveyors' (1830's) records (Tans 1976), soil cores, well-developed *C. stricta* tussocks (Costello 1936), long-term flooding patterns on the Wisconsin River (Department of the Army, Chicago District Corps of Engineers 1972), 1949 air photographs, and early description indicate that densely vegetated perennial wetland plant communities probably have occupied the site for at least the last century.

Water level changes significantly affected $\sim$ 75% of the study area by 1977. The area significantly affected by waste heat is more difficult to define. The physiological and phenological data for *C. lacustris* and *T. latifolia* showed adverse effects from waste heat occurring within 100 m of the wet dike in 1977 and apparent subsidy effects on *Typha* at distances up to 300 m from the dike.

Vegetation changes on the Columbia site occurred almost immediately. Changes were obvious and evident in the field at community and population levels within 1 yr after the station began operation in spring 1975. Effects of flooding were seen in the summer 1975 data. Late flowering and delayed dieback of individual plants occurred in localized areas near the dike in fall 1975. Major phenological changes were evident within 100 m of the dike by spring 1976. Significant changes in population density and community structure occurred in all communities by summer 1976.

A predominant trend of decreasing species richness and diversity was observed from 1974 to 1977. However, no uniform relationship existed between diversity and intensity of disturbance--neither species richness nor distribution of their abundances. Although obvious changes in community structure took place from 1974 to 1977, the ecological signficance of different community patterns of response was not evident from the diversity data alone. Disturbance did not simply increase or decrease diversity. Species richness, diversity, and equitability sometimes varied independently. All of the diversity measures used decreased in most cases, but increased in others, and frequently did both during the period from 1974 to 1977 as the spatial distribution and intensity of disturbance increased on the Columbia site. Differences observed between communities in diversity measures were related to the differential sensitivity of spatially dominant species to disturbance. Where disturbance was of the type to which dominant species were sensitive, diversity and equitability increased as new or competitively inferior species colonized or spread to space made available by the decline of previously dominant populations. Diversity and equitability decreased where disturbance favored one or two dominant species.

C. lacustris exhibited much greater sensitivity to stress than *T. latifolia*. Population data showed an almost uniformly negative response by *C. lacustris*, but both positive and negative responses by *T. latifolia*. *Typha* exhibited a clear positive response to elevated water levels, increasing its density where it had been abundant and expanding its distribution substantially by 1977. Adverse effects on *Typha* were restricted to limited areas where temperature increases were > 7 to 16°C and occurred in winter. Viable populations of *C. lacustris* persisted only in areas where temperature increases were negligible throughout the year.

Physiological and phenological data from laboratory and field experiments related the response of *T. latifolia* and *C. lacustris* to altered seasonal patterns of carbohydrate storage and shoot phenology induced primarily by groundwater temperatures out of phase with normal cycles of plant growth. In addition to establishing the causal mechanism relating vegetation changes to leakage from the cooling lake, this data set identified field signs of heat stress and suggested general species characteristics that may be useful indicators of potential sensitivity to stress.

Phenological changes appear to be reliable indicators of heat stress. Although changes in population density occurred throughout the study area, obvious phenological changes were not observed outside the area affected by altered temperature patterns. In areas receiving waste heat, individual plants showed visible signs of stress before the population collapsed. Where the species grew in dense stands, the symptoms were visible to the naked eye at distances up to 300 m. In general, phenological changes became evident 1 yr before population density was reduced and 2 yr before the population collapsed.

Characteristics of plants experiencing heat stress that were observable and easily measured in the field included: 1. Unseasonable chlorosis, 2. reduced height of mature shoots, 3. increased height of new spring and fall shoots, and 4. early or delayed shoot emergence at reduced density.

RECOMMENDATIONS

The concept of life history strategy warrants further consideration as a theoretical tool for predicting species sensitivity to disturbance and assessing the probable effects on wetland plant communities. The physiological and phenological data for *C. lacustris* and *T. latifolia* suggested that the likelihood of predicting the response of dominant species would be enhanced by knowing the key characteristics of its life cycle. The extreme sensitivity of *C. lacustris* appeared to be a consequence of its particular life history cycle and the timing, as well as the magnitude, of the disturbance. Species characteristics that may serve as useful indicators of potential sensitivity to stress include life span, the seasonal schedule of various phenophases, seasonal distribution of biomass between above- and below-ground parts, ability to regenerate or colonize, and reproduction and mortality schedules.

Research should be continued on the Columbia site in order to take advantage of the long-term (1974 to present) data base and monitor the eventual outcome of a sustained perturbation on wetland vegetation. The 1974 to 1977 data address but cannot answer the questions regarding establishment of an equilibrium community or recovery following disturbance. Examination of temporal patterns in both the population and community data reveals that the Columbia wetlands are still in a phase of transient behavior that should continue to be monitored. Further changes can be expected at both the population and community levels. In terms of environmental factors, the Columbia wetlands are only 33% through a predicted transient. Although water levels have more or less stabilized, temperatures are expected to increase in magnitude and spatial extent after 1978 as the heat load of the second Columbia unit is added to the cooling lake (Andrews 1978b). The results of 1974 to 1977 population data and 1977 physiological data for the Columbia site indicate that dominant perennial populations of rhizomatous sedges and grasses will continue to decline. As they do, the structure of the community will continue to change. In areas subject to minimal temperature increases tolerant hydrophytic species such as *T. latifolia* probably will become dominant. Areas subject to maximum temperature increase may support only annual vegetation or remain as unvegetated exposed muck or open water.

Future research should address the system-level consequence of change in the vegetative component. The development of effective management and assessment tools depends on the identification and understanding of critical system components and interactions. Field observations on the Columbia site indicate that increased erodibility of the peat mass may be associated with the transition in dominants from perennial to annual and from persistent to non-persistent species. Changes in species numbers and diversity values appear to be less relevant than changes in the life history characteristics of spatially dominant species. Further research should address the problem of identifying appropriate analytical categories and the components and processes of wetland systems critical to effective environmental impact assessment. The data from this study suggest that grouping species with similar sets of life history traits may identify meaningful aggregate variables between the level of the individual plant species and the community.

Activities which alter physical inputs to wetlands are likely to continue to occur as the result of energy-related developments. More effective tools and paradigms of analysis for predicting short- and long-term effects of environmental changes on wetland plant communities are more likely to come from research based on demographic principles than on existing community theories of succession or diversity. Studies on the Columbia site showed no evidence of the community by community replacements predicted by the succession model and no fixed relationship between disturbance and diversity measures. Future research should include studies of: 1. The population biology of important wetland species including temporal life history characteristics, seasonal changes in population age/size structure, and germination requirements [Bernard and Gorham (1978) Van der Valk and Davis (1976a, 1978) have already undertaken studies in this area]; the relationship between population characteristics and the type, severity, and periodicity of naturally occurring fluctuations in the physical environment; and 3. the relationship of life history characteristics to the probability of extinction and to the capacity to regenerate or recolonize under human-induced fluctuations in the physical environment.

SECTION 3

WETLAND PLANT POPULATION AND COMMUNITY RESPONSES TO ALTERED TEMPERATURE AND FLOODING PATTERNS

INTRODUCTION

Research Objectives

The wetland plant ecology study of the Columbia Project was undertaken in 1974 to monitor vegetation changes associated with leakage from the cooling lake (Green 1979, cf. Cairns 1980). Although it was known when the study began that the sedge meadow and shallow marsh west of the lake would be affected by elevated groundwater levels and temperature increases caused by leakage, uncertainty existed regarding the nature and probable timing of the environmental and vegetation changes expected. The principal objective of the wetland research was to determine how wetland plant populations and communities might change in response to heat and water stress.

Hypothesis

It was hypothesized that changes in water levels and water temperature caused by seepage from the cooling lake would lead to significant changes in wetland plant populations and communities. In the framework of this general hypothesis, five basic questions were examined during the monitoring program. These are stated in section 1.

Two factors constrained more specific formulation of hypotheses and sampling design: 1. The spatial scale, temporal distribution, and magnitude of the expected environmental changes were not known when sampling began, 2. empirical evidence and theoretical understanding of the effects of exogeneous disturbances on wetland vegetation dynamics were limited. A general trend from sedge meadow and shallow marsh species toward more hydrophytic species could be expected for the Columbia site if water levels increased sufficiently. The critical relationship between wetland vegetation and the frequency, range, and duration of water level fluctuations seasonally and from year to year has been well established (Kadlec 1962, Harris and Marshall 1963, Sculthorpe 1967, Walker and Wehrhahn 1971, Auclair et al. 1973, Weller and Fredrickson 1974, Van der Valk and Davis 1976b and 1978b, Gosselink and Turner 1978). However, since the magnitude of the increase was not known and the elevation of the meadow and marsh covered a range of more than 60 cm, the magnitude and rate of change in the vegetation and the size of the area that might be affected by water level changes could not be predicted. The effects of waste heat on aquatic systems also have been studied extensively (Krenkel and Parker 1969, Coutant 1973, Gibbons and Sharitz 1974a and 1974b). However, at the time this research was initiated, few studies had addressed the question of thermal effects on vascular aquatic plants (Anderson 1969, Wood and Zieman 1969, Sharitz et al. 1974, Young 1974). No studies existed on northern freshwater wetland plant populations or communities. Furthermore, neither the magnitude, temporal patterns, or spatial extent of temperature changes on the site was known. Small increases in temperature might act as a subsidy rather than a stress on the system (Odum 1974, Gibbons 1976, Odum et al. 1979).

The monitoring program on the Columbia site provided a unique opportunity to examine some fundamental empirical and theoretical questions about the response of wetland plant populations and communities to exogenous disturbances. The principal theoretical paradigms regarding vegetation change in wetlands, succession, and diversity theory were questioned, especially with respect to environmental impact assessment. Several authors have suggested that the concepts of static stability and diversity generally associated with classical succession theory (Clements 1916, Tansley 1939) are of limited use in interpreting or predicting the effects of anthropogenic disturbance on ecosystems (Loucks 1970, Holling 1973, Botkin and Sobel 1975, Green 1979). Although diversity measures are widely used among environmental biologists (Cairns 1974, Weber 1973, States et al. 1978, Darnell et al. 1976), little agreement could be found on their meaning or relationship to successional status or response to disturbance (Goodman 1975). The general succession model was criticized (Drury and Nisbet 1971 and 1973, Horn 1974) and its validity in terms of controlling factors, predicted sequence, direction, and rates of change for wetlands in particular was questioned (Weller and Spatcher 1965, Walker 1970, Heinselman 1970, Van der Valk and Bliss 1971, Weller and Fredrickson 1974, Bedford et al. 1974). The limited empirical evidence available for wetland systems does not support the presumed relationship between diversity and disturbance, either naturally-occurring (Van der Valk and Bliss 1971, Van der Valk and Davis 1976b) or anthropogenic (Sharitz et al. 1974). The types of vegetation changes predicted by the succession model are those regulated by autogenic processes taking place in the system as a result of species interactions under equilibrium conditions. Response to disturbance is regarded as a function of community complexity and stability, seen as increasing together with "advance" in successional stage, and measured as species diversity (Odum 1969, Margalef 1968, Caswell 1976). The types of vegetation changes which were of concern in this study were those that might be caused by external influences. They would occur under non-equilibrium conditions and would likely reflect individual species-environment relationships as well as biotic interactions and community processes.

Reported herein are changes observed in wetland plant populations and community characteristics at the Columbia site from 1974 to 1977 together with the relationship between the response of dominant species and changing diversity patterns.

METHODS

Vegetation Sampling

Changes in species occurrence and plant community composition and structure were monitored semiannually from 1974 to 1977, by identification and stem counts of all plant species in 0.25 m^2 quadrats. Quadrats were located by reference to a regular 50 x 50 m grid system laid out within well-defined sedge meadow/marsh boundaries. In 1974, permanent station markers were placed at 50 m intervals along 40 linear transects running approximately perpendicular to the west dike of the cooling lake. In 1976, transects and stakes were added at 25 m intervals between transects 18 and 28 to intensify sampling in areas of apparent major environmental change. For each sampling period, counts were taken in quadrats placed 1 or 2 m from the permanent stake in a random choice of two of the four directional quadrants. The stake marked the intersection of the quadrant boundaries.

Stations were sampled during summer and fall of each year from 1974 to 1977. In each quadrat, plant species were identified and counted as number of stems or culms. Counts of *Lemna minor* were recorded as absent (0), sparse (25), moderate (50), or dense (75). Exceptions to the general sampling procedure are: In 1975 and fall 1976 only the presence or absence of species were recorded for ∿33% of the total sample. Only transects 18 to 30 were sampled in summer 1976 and 1977. From summer 1976 through fall 1977 the sampling interval for environmental factors between transects 18 and 28 was based on a 25 x 25 m grid rather than a 50 x 50 m grid. Frequent field observations, ground photographs, color air photographs, and color infrared air photographs (Wynn and Kiefer 1977) were used to supplement field measures.

Plant nomenclature follows Gray's Manual (Fernald 1950). Species present in the study area are enumerated in Kiefer et al. (1976). Plant specimens were deposited in the University of Wisconsin Herbarium for verification.

Mapping

Two vegetation maps were prepared using conventional air photograph interpretation and field data. The base map was a 1974 photographic map of the site, prepared and corrected by the Wisconsin Department of Transportation to a topographic map with 2-ft contour intervals. Air photographs from 1975 and 1977 were projected onto the base map and corrected to cultural features. Vegetation patterns visible on the air photographs were outlined and identified by a combination of field checks and references to sampling data.

The maps represent the distribution of visually prominent assemblages (Curtis 1959) of plant species. Boundaries are necessarily arbitrary and shift with seasons (Buchanon and Scarpace 1980); the communities intergrade with each other. Visually distinct communities may or may not be ecologically significant (Greig-Smith 1964).

Environmental Factors

Changes in environmental factors prevailing in the meadow/marsh west of the Columbia cooling lake were studied in two subprojects of the Columbia Study: The Hydrogeology Group assessed alterations in three parameters of the groundwater system: 1. The quantity of groundwater flow into the wetland and the surface water levels in the wetland, 2. the temperatures of groundwater and surface water, and 3. the quality of groundwater and surface water as expressed by concentrations of commonly occurring anions and cations. Field data were used to develop and test models to similate groundater flow before and after filling the cooling lake and long-term seasonal temperature patterns in the wetland west of the cooling lake (Andrews 1976, Stephenson and Andrews 1976, Andrews and Anderson 1978, Andrews 1978a, 1978b, and 1980).

The Wetland Plant Ecology Group collected data on water depths, substrate temperatures, and surface water temperatures in each quadrat during semi-annual vegetation samplings. Two water depths were recorded: 1. Depth to plant rooting zone, measured as the distance between water surface and the top of the soil surface in which plants were rooted, and 2. depth to solid substate, measured as the distance between water surface and the top of the substrate capable of supporting the recorder's weight. Data measures were taken with a wooden meter stick marked to 0.1 cm. Substrate temperatures were measured ∿ 15 cm below the soil surface in which plants were rooted, i.e., in the plant rooting zone. Surface water temperatures were recorded at 15 cm below the water surface or just above the soil surface if water depth was < 15 cm. Temperatures were measured using a glass-mercury thermometer or a Reotemp Inc. 60-cm metal probe thermometer.

RESULTS

Plant Communities Prior to Disturbance

Prior to significant environmental change, the study area consisted of three basic vegetation types: 1. Sedge meadow, 2. emergent aquatic or shallow marsh, and 3. lowland shrubs (Curtis 1959, Wisconsin Department of Natural Resources 1973). The sedge meadow category included two areas distinguished on the basis of the prominence of well-developed tussocks of *Carex stricta* or dense stands of *Carex lacustris*. The area of emergent aquatic vegetation was distinguished by the prominence of *Typha latifolia* or *Scirpus fluviatilis* in the canopy. A transition community between distinct sedge meadow and emergent aquatic zones contained understory species from the emergent aquatic zone and prominent overstory species from the sedge meadow zone. Areas of lowland shrubs were characterized by the prominence of *Spiraea alba* with understory species closely resembling the sedge meadow areas, especially the *C. stricta* dominated meadow, or by a mix of shrubs (*Salix* spp. and *Cornus stolonifera*) with lowland trees. Thus, six visually distinctive plant communities were defined.

Mapping was used to define approximately the broad spatial distribution of the six plant communities. Sampling data were used to characterize the species composition and structure of each community. The map of 1975 vegetation patterns is shown in Figure 3. Note that in addition to the six basic plant communities, areas obviously dominated by *Calamagrostis canadensis, Scirpus fluviatilis*, or *Sparganium eurycarpum* are mapped separately. The latter two, along with open water areas, are combined with the emergent aquatic community for data analysis. The *C. canadensis* areas are considered part of the *C. stricta* community. The map also separates shrub areas consisting of a mix of *Salix* spp. and *C. stolonifera* with some *S. alba* from similar shrub areas which also contain lowland trees such as *Populus deltoides, Ulmus americana, Betula nigra, Acer saccharinum*, and *Populus tremuloides*. For data analysis the two are pooled. Because of the small size of the quadrats (0.25 m^2), the species sampled largely reflect the understory composition of shrub and tree communites.

For purposes of data analysis, each sampling station in the grid system was assigned to one of the six communities. Assignment was based on vegetation patterns and shown on the 1975 map and on field data. If a station fell within a locally abundant patch of *C. lacustris* within a largely *C. stricta* area, it was assigned to the *CAREX STRICTA* community. The six plant communities are defined as follows:

1. The *CAREX LAUSTRIS* community consists of areas with dense stands of *C. lacustris* visually prominent in the canopy, with *C. stricta, C. canadensis*, and *Sagittaria latifolia* locally abundant.

2. The *CAREX STRICTA* community is made up of areas with numerous well-developed tussocks of *C. stricta* or *C. canadensis* visually prominent in the canopy, mixed with other sedges, grasses, forbs, and ferns. *C. canadensis, C. lacustris, S. latifolia*, and *Spartina pectinata* were locally abundant. For purposes of data analysis, areas mapped as prominent *C. canadensis* areas are pooled with this group.

3. The EMERGENT community is dominated by tall, robust, emergent aquatic vegetation, such as *T. latifolia, Scirpus fluviatilis*, and *S. eurycarpum. Carex rostrata, C. lacustris, S. latifolia*, and *Acorus calamus* are locally abundant.

4. The TRANSITION community is a mixed transition zone between distinct sedge meadow and emergent aquatic plant assemblages. *C. rostrata, C. canadensis, C. lacustris, C. stricta*, and *S. latifolia* are locally abundant.

5. The *SPIRAEA* community occupies areas with the shrub, *Spiraea alba*, prominent in the overstory, and with an understory similar to, but less dense than, *CAREX STRICTA* areas.

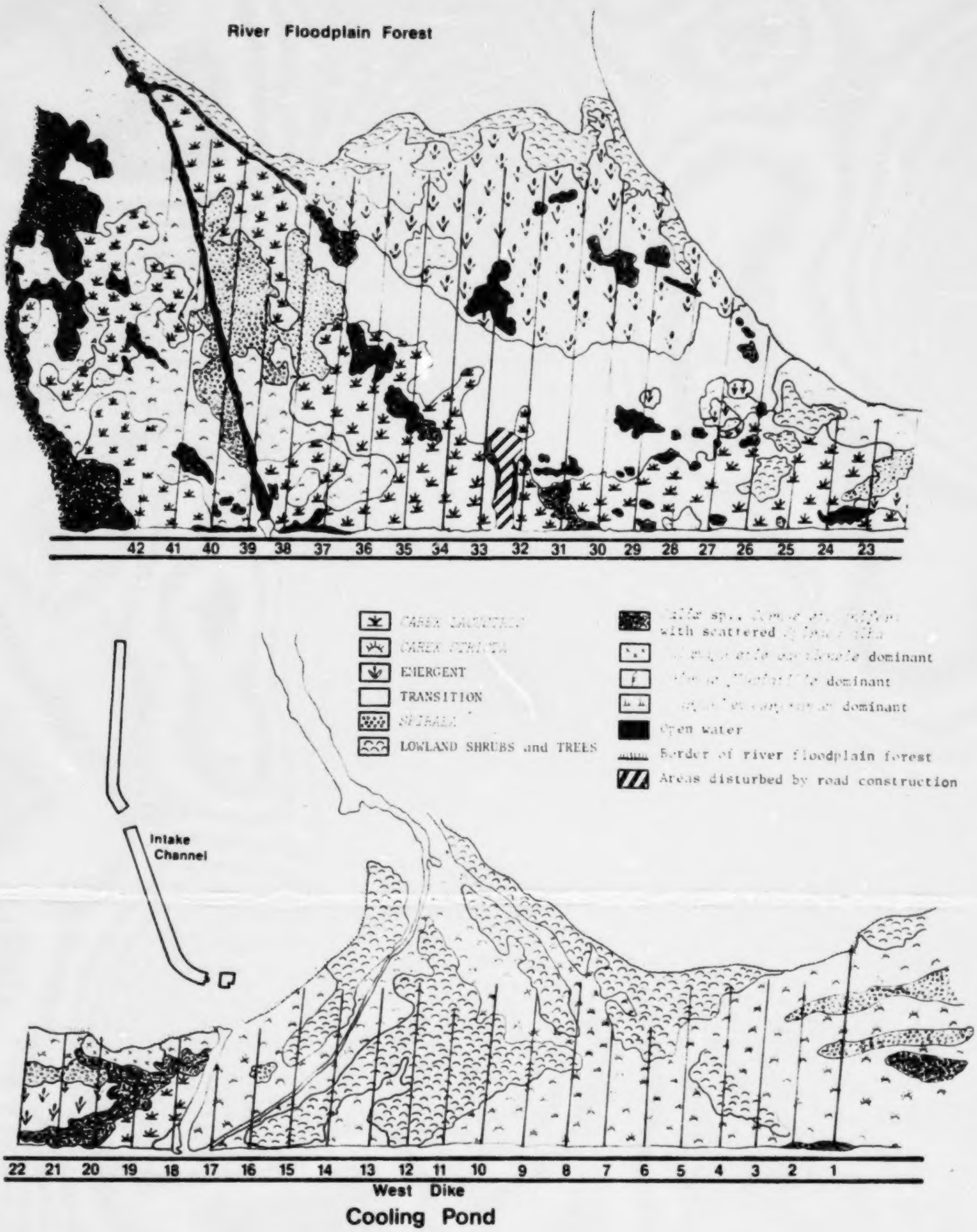
River Floodplain Forest
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
CAREX LACUSTRIS
CAREX STRICTA
EMERGENT
TRANSITION
SPIRAEA
LOWLAND SHRUBS and TREES
Salix sp.,
with scattered
dominant
dominant
dominant
Open water
Border of river floodplain forest
Areas disturbed by road construction
Intake Channel
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
West Dike
Cooling Pond

Figure 3. Vegetation map showing distribution of wetland plant communities in 1975.

6. The MIXED SHRUBS and LOWLAND TREES community comprises two areas, namely, areas with mixed shrub species (*Salix* spp. and *C. stolinfera* with some *S. alba*) prominent in the overstory, and areas of mixed shrubs containing scattered lowland trees such as *P. deltoides, U. americana, B. nigra, A. saccharinum*, and *P. tremuloides*.

Areas disturbed by construction activity were mapped but not analyzed.

The six plant communities actually represent a single complex of wetland plant communities which form a continuum (Gleason 1939, Curtis 1959) of intergrading types. Many of the major species are distributed throughout the area with all of the communities sharing numerous species. They can be distinguished on the basis of physiognomy (shrubs, tall robust emergents, non-sedge/grass emergents, sedges, and grasses), comparative abundance of dominant species, and average water depth.

Table 1 lists the plant species composition, absolute density, relative density, and total number of species for the six communities in summer 1974. Note that three of the species (*C. stricta, C. Lacustris*, and *C. canadensis*) occur in the top seven ranked species in all communities. The *CAREX STRICTA* community assemblage had the greatest number of species (58) and the TRANSITION zone the fewest species (35).

Environmental Changes

The principal physical characteristics examined on the Columbia site were the hydrologic regime and the thermal regime. The chemical characteristics of surface and groundwater flows on the site also were monitored (Andrews 1978b).

Hydrologic Regime--

Four important attributes of the hydrologic regime have been altered in the Columbia wetlands (Gosselink and Turner 1978): 1. Source, 2. quantity, 3. velocity, and 4. timing. In 1975, the cooling lake replaced the regional watershed as the source of water to the wetlands. Leakage occurred through the walls of the dike and from the bottom of the lake through the peat bed (Figure 4). Consequently, groundwater discharge rates increased by a factor of six times with subsequent changes in surface water flow (velocity) and water level fluctuation (timing or frequency of inundation and its regularity) (Andrews 1978b).

Prior to filling the lake, the sources of groundwater discharging on the site were upland areas to the east and southeast and knolls on the site. Precipitation provided the greatest supply of water, $\sim$ 76 cm/yr. Good internal drainage and a constant exchange of water kept water quality in the wetlands high. Precipitation and groundwater discharge together usually exceeded evapotranspiration, except at the height of the growing season when evapotranspiration exceeded water supply. At that time water levels in the wetlands were drawn down, and water flow out of the wetlands almost ceased. Throughout the year water levels fluctuated widely due to

TABLE 1. PLANT SPECIES COMPOSITION, ABSOLUTE DENSITY (D) AND RELATIVE DENSITY (RD) FOR SIX PLANT COMMUNITIES IN SUMMER, 1974 (T. 1-40)

CAREX LACUSTRIS			*CAREX STRICTA*			EMERGENTS		
Species	(D)	(RD)	Species	(D)	(RD)	Species	(D)	(RD)
Carex stricta	333	.226	*Carex stricta*	698	.349	*Carex rostrata*	270	.365
Carex lacustria	229	.156	*Calamagrostis canadensis*	265	.133	*Carex lacustris*	138	.186
Calamagrostis canadensis	168	.114	*Lemna minor*	150	.000	*Sagittaria latifolia*	112	.151
Dryopteris thelypteris	151	.103	*Sagittaria latifolia*	129	.064	*Lemna minor*	84	.000
Pilea pumila	145	.099	*Bidens coronata*	116	.058	*Galium* sp.	33	.045
Bidens coronata	109	.074	*Leersia oryzoides*	92	.04	*Acorus calamus*	29	.039
Aster simplex	37	.025	*Dryopteris thelypteris*	85	.043	*Calamagrostis canadensis*	20	.027
Onoclea sensibilis	30	.020	*Carex lacustris*	84	.042	*Typha latifolia*	17	.023
Sagittaria latifolia	29	.020	*Pilea pumila*	81	.041	*Polygonum hydropiperoides*	17	.023
Lysimachia thyrsiflora	27	.018	*Lycopus uniflorus*	57	.029	*Stellaria longifolia*	16	.022
Campanula aparinoides	22	.015	*Galium* sp.	38	.019	*Lysimachia thyrsiflora*	13	.018
Galium sp.	18	.012	Unknown	37	.019	*Scirpus fluviatilis*	12	.016
Mentha arvensis	18	.012	*Carex rostrata*	36	.018	*Scutellaria galericulata*	11	.015
Leersia oryzoides	17	.012	*Juncus brachycephalus*	29	.014	*Carex aquatilis*	10	.014
Carex aquatilis	15	.010	*Lysimachia thyrsiflora*	29	.014	*Carex prairea*	7	.009
Carex rostrata	15	.010	*Spartina pectinata*	28	.013	*Sparganium eurycarpum*	6	.007
Scutellaria galericulata	15	.010	*Salix petiolaris*	20	.010	*Lycopus americanus*	3	.003
Lycopus uniflorus	11	.007	*Mentha arvensis*	20	.010	*Lycopus uniflorus*	3	.003
Typha latifolia	9	.006	*Campanula aparinoides*	17	.009	*Rorippa islandica*	3	.003
Spiraea alba	8	.005	*Phalaris arundinacea*	16	.008	*Iris shrevii*	2	.002
Lycopus americanus	8	.005	*Polygonum sagittatum*	14	.007	*Rumex orbiculatus*	2	.002
Aster lucidulus	7	.005	*Boehmeria cylindrica*	11	.005	*Rumex verticillatus*	2	.002
Rumex orbiculatus	6	.004	*Aster simplex*	10	.005	*Spiraea alba*	2	.002
Agropyron repens	5	.003	*Rumex orbiculatus*	9	.004	*Aster simplex*	2	.002
Helenium autumnale	5	.003	*Onoclea sensibilis*	8	.004	*Campanula aparinoides*	2	.002
Polygonum sagittatum	4	.003	*Lycopus americanus*	8	.004	*Sium suave*	2	.002
Polygonum natans	4	.003	*Carex aquatilis*	7	.003	*Carex stricta*	1	.001
Polygonum coccineum	3	.002	*Potentilla palustris*	7	.003	*Scirpus validus*	1	.001
Aster sp.	3	.002	*Polygonum hydropiperoides*	6	.003	*Nquisetum fluviatile*	1	.001
Cicuta bulbifera	3	.002	*Triadenum virginicum*	6	.003	*Alisma plantago-aquatica*	1	.001
Eupatorium perfoliatum	2	.001	*Eupatorium maculatum*	5	.002	*Scutellaria lateriflora*	1	.001
Convolvulus sepium	2	.001	*Cicuta bulbifera*	5	.002	*Veronia fasciculata*	1	.001
Salix petiolaris	2	.001	*Helianthus grosseserratus*	4	.002	S=32, N=38		
Solanum dulcamara	2	.001	*Polygonum coccineum*	4	.002			
Lemna minor	1	.000	*Vicia americana*	4	.002			
Rumex verticillatus	1	.001	*Helenium autumnale*	3	.001			
Lysimachia terrestris	1	.001	*Stellaria longifolia*	3	.001			
Polygonum sp.	1	.001	*Polygonum natans*	2	.001			
Ludwigia palustris	1	.001	*Aster lucidulus*	2	.001			
Stellaria longifolia	1	.001	*Aster puniceus*	2	.001			
Veronia fasciculata	1	.001	*Acorus calamus*	1	.000			
S*=41, N=40			*Spiraea alba*	1	.000			
			Veronica scutellaria	1	.000			
			Viola cucullata	1	.000			
			S=44, N=46					

Continued

(Table 1) continued

TRANSITION			*SPIRAEA*			LOWLAND TREES AND SHRUBS		
Species	(D)	(RD)	Species	(D)	(RD)	Species	(D)	(RD)
Calamagrostis canadensis	138	.152	*Carex stricta*	91	.228	*Calamagrostis canadensis*	15	.214
Carex stricta	135	.149	*Pilea pumila*	91	.228	*Onoclea sensibilis*	12	.171
Carex rostrata	133	.147	*Dryopteris thelypteris*	41	.103	*Pilea pumila*	10	.143
Polygonum hydropiperoides	117	.129	*Calamagrostis canadensis*	24	.060	*Aster simplex*	8	.114
Carex lacustris	71	.078	*Onoclea sensibilis*	24	.060	*Carex stricta*	3	.043
Pilea pumila	69	.076	*Carex lacustris*	21	.053	*Geranium maculatum*	3	.043
Sagittaria latifolia	64	.071	*Salix petiolaris*	12	.030	*Eupatorium maculatum*	2	.029
Dryopteris thelypteris	26	.030	*Spiraea alba*	10	.025	*Spiraea alba*	2	.029
Polygonum coccineum	20	.023	*Boehmeria cylindrica*	10	.025	*Aster puniceus*	2	.029
Spiraea alba	20	.023	*Lycopus americanus*	9	.023	*Lycopus americanus*	2	.029
Campanula aparinoides	20	.023	*Polygonum coccineum*	8	.020	*Cornus racemosa*	2	.029
Galium sp.	17	.020	*Galium* sp.	8	.020	*Salix bebbiana*	2	.029
Polygonum natans	15	.018	*Iris shrevii*	7	.018	*Carex lacustris*	1	.014
Lysimachia thyrsiflora	13	.015	*Lycopus uniflorus*	7	.018	*Asclepias incarnata*	1	.014
Scutellaria galericulata	11	.013	*Sagittaria latifolia*	6	.015	*Rumex orbiculatus*	1	.014
Rumex orbiculatus	6	.007	*Spartina pectinata*	4	.010	*Galium* sp.	1	.014
Sparganium eurycarpum	6	.007	*Sium suave*	4	.010	*Mentha arvensis*	1	.014
Triadenum virginicum	5	.006	*Rumex orbiculatus*	3	.008	*Polygonum sagittatum*	1	.014
Onoclea sensibilis	4	.005	*Lysimachia thyrsiflora*	3	.008	*Ludwigia palustris*	1	.014
Lycopus uniflorus	4	.005	*Aster puniceus*	2	.005	S=19, N=4		
Lysimachia terrestris	3	.004	*Mentha arvensis*	2	.005			
Carex aquatilis	2	.002	*Polygonum sagittatum*	2	.005			
Lycopus americanus	2	.002	*Scutellaria galericulata*	2	.005			
Polygonum sagittatum	2	.002	*Viola cucullata*	2	.005			
Convolvulus spithamaeus	1	.001	*Rumex verticillatus*	1	.003			
Veronica scutellata	1	.001	*Campanula aparinoides*	1	.003			
S=26, N=28			*Cicuta bulbifera*	1	.003			
			Stachys palustris	1	.003			
			Vicia americana	1	.003			
			Bidens coronata	1	.003			
			S=30, N=10					

*S=total number of species, N=number of quadrats sampled.

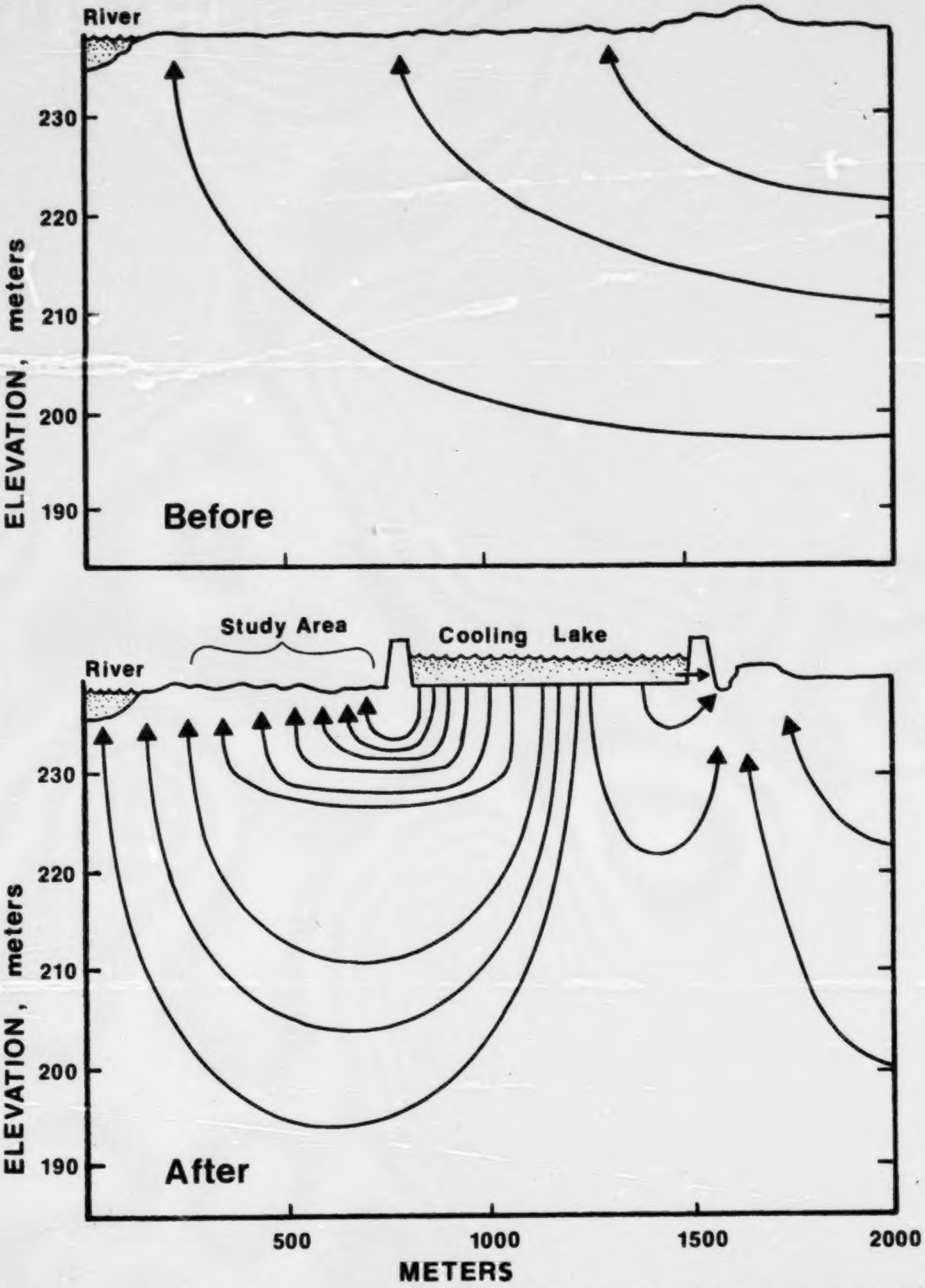
River
230
220
210
200
190
ELEVATION, meters
Before
Study Area
Cooling Lake
River
230
220
210
200
190
ELEVATION, meters
After
500
1000
1500
2000
METERS

Figure 4. Study area showing configuration of groundwater flow system before and after filling of the cooling pond (modified from Andrews 1978b).

spring floods, growing season drawdowns, and water level recovery when the growing season ended (Stephenson and Andrews 1976).

After filling the lake, the total groundwater supply to the wetlands from leakage greatly exceeded precipitation and evapotranspiration. In 1976 groundwater discharge averaged 305 cm/yr near the dike, with rates as high as 760 cm/yr in some places. The major zone of groundwater discharge is shown in Figure 5.

Changes in water depth and fluctuation patterns due to increased rates of groundwater discharge were evident immediately. Water level increased an average of 10 cm (Andrews and Anderson 1978). More significantly, water levels stabilized (Figure 6). This is due to the fact that water supplied from the cooling lake is constant and the fraction removed by evapotranspiration is small compared to the total amount of water supplied by leakage. It is clear from Andrew's data on water levels (Andrews and Anderson 1980), known elevation points within the marsh, and monthly field observations, that almost all stations have been continuously saturated or inundated and, therefore, are anaerobic except for a thin, oxidized layer at the surface (Gambrell and Patrick 1978) since early 1975. Of 20 water depth measures taken in August 1973 (late summer when evapotranspiration is high), only one showed water standing above the peat surface.

Prior to filling the lake, no surface water flow was apparent in the meadow/marsh except for minor flow in two ditches. In winter the entire area was frozen and covered with snow. Flow is now evident in many parts of the area, with rates high enough to maintain continuous open water during winter months (Figure 7). Other changes in the physical characteristics of the study site occurred as a result of increased rates of groundwater discharge. Continuous flooding and high hydrostatic pressures caused expansion of the peat and lifting or floating up of the surface and root layer. Thus the effective water depth for plants is frequently less than the averge increase in water depth. The proportion of quadrats sampled with a floating surface layer increased from 1.3% in 1975 to 70.4% in 1977.

Increased and continuous surface water flows have resulted also in the development of flow channels and substrate erosion. As expected, the principal flow channels developed within the areas of highest groundwater discharge. They are most evident in winter (Figure 7) and remain largely unvegetated throughout the year.

The combined effects of peat lifting, substrate erosion, and channel development have altered the microtopography of the peat surface. The variation in surface topography was smoothed in places and accentuated in others.

Direct hydrologic effects on the Columbia wetlands of leakage from the cooling lake thus include: 1. Increased groundwater discharge, 2. nearly constant water levels, 3. higher water levels, and 4. increased surface water flows. Secondary effects on the wetlands include: 1. Expansion and Lifting of the peat, 2. development of flow channels, 3. substrate erosion,

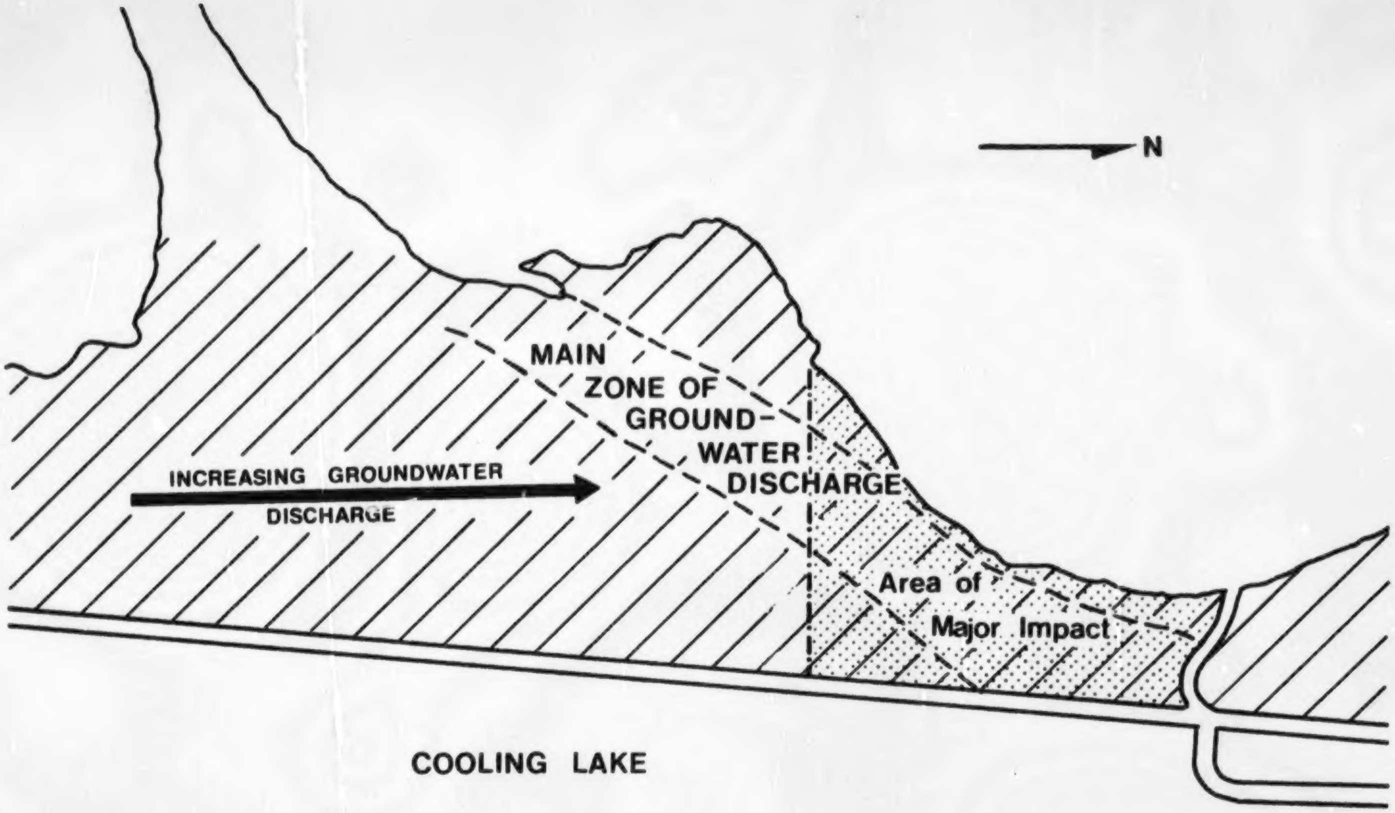
N
MAIN
ZONE OF
GROUND-
WATER
DISCHARGE
INCREASING GROUNDWATER
DISCHARGE
Area of
Major Impact
COOLING LAKE

Figure 5. Groundwater discharge patterns in the wetlands (modified from Andrews 1976).

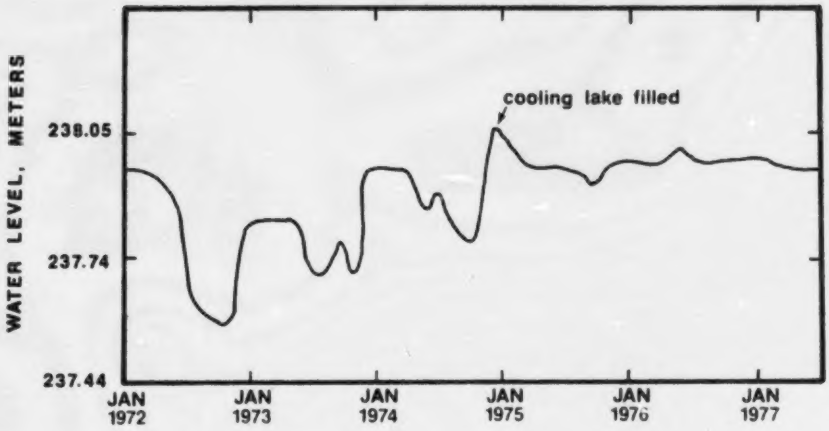

Figure 6. Water level fluctuations in the wetland west of the cooling pond before and after filling of the cooling pond (from Andrews 1978b). Marsh elevation varies from 237.26 to 238.20 m.

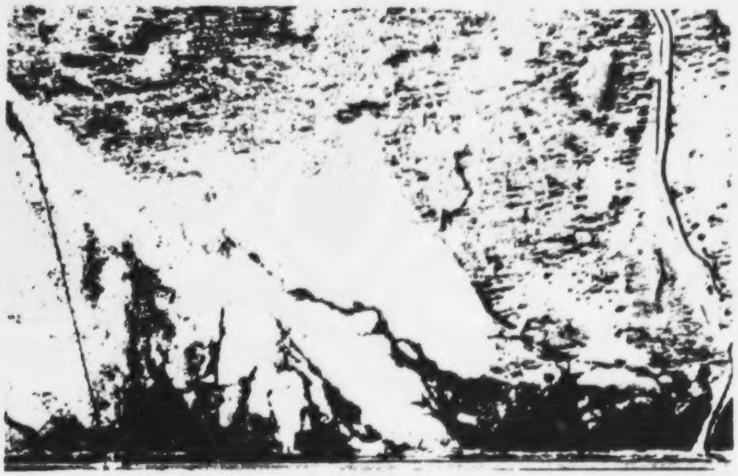

Figure 7. Aerial photograph of meadow/marsh showing open water areas on 1 March 1976. White areas are snow-covered. Lower edge of photograph shows the west dike of the cooling lake. Area shown is between transects 18 and 40.

4. changes in substrate microtopography, and 5. alteration of winter ice formation patterns.

No significant changes in the ionic composition of the groundwater were noted in the study area. Chemical characteristics of surface and groundwater flows on the site are given in Table 2 (Andrews 1976). These do not differ greatly throughout the wetland area (Andrews 1976).

Thermal Regime--

Leakage from the cooling lake has significantly altered the thermal regime of the wetlands in the study area. In general, groundwater temperatures are warmer and out of phase with normal cycles of plant growth (Figure 8).

Prior to filling the lake, the temperature of the groundwater discharging to the wetlands remained fairly constant throughout the year at ∿ 10°C. Presently, the temperatures reflect the annual temperature variation in the cooling lake (1 to 30°C). However, the temporal and spatial distributions of water temperature changes in the wetland west of the cooling lake are complex. The location and time of occurrence of the seasonal maximum and minimum groundwater temperatures in the wetland are functions of distance from the cooling lake and the distribution of subsurface materials as well as lake temperature patterns. Because water moving from the lake to the wetland passes through the subsurface materials, water temperatures in the wetland lag behind those of the cooling lake. Because subsurface materials are not homogeneous in permeability, depth, or spatial distribution, the time lag is not distributed uniformly with distance from the dike. In general, the time lag between the occurrence of maximum groundwater temperature and maximum cooling lake temperature gradually increases, and the amplitude of the fluctuation between maximum and minimum temperatures decreases with distance from the dike (Figure 8) (Andrews 1978b). Significant temperature changes are confined to an area within 100 m of the dike. However, where the peak layer is thickest or where a layer of pronounced low permeability material occurs below the peat, temperature patterns are attenuated or may resemble control areas, even though the area is within 100 m of the dike.

The most significant departures from normal temperature patterns occur near the dike where a pronounced low permeability layer does not exist beneath the surface. In these areas, flow through the groundwater system is fairly rapid. From 1975 to 1976, temperatures of the groundwater discharging near the dike lagged behind temperatures in the cooling lake by 4 to 8 months. This lag resulted in cold water (< 3°C) discharging into the wetland during spring 1975 and warm water discharging during the late fall and early winter (19 to 24°C) (Andrews 1976).

Area of Major Impact--

Environmental change has been most pronounced and rapid near the lake where flow rates of groundwater coming from the cooling lake are highest. In general, substrate temperature variation, departure from normal temporal

TABLE 2. CHEMICAL CHARACTERISTICS OF WATER AT THE COLUMBIA SITE (FROM ANDREWS 1976)

Parameter	Groundwater	Sedge meadow	Cooling lake	Wisconsin River
TDS[a], mg/liter	200	230 (variable)	260	145
Mg, mg/liter	21	> 20	10	5.1
Ca, mg/liter	21	—	35	18
SO_4, mg/liter	7	10	154	86
NO_3, mg/liter	< 0.01	< 0.01	0.7	0.4
PO_4, mg/liter	< 0.02	< 0.02	0.2	0.1
Na, mg/liter	10	17	29	16
pH		7.4		

[a] Total dissolved solids.

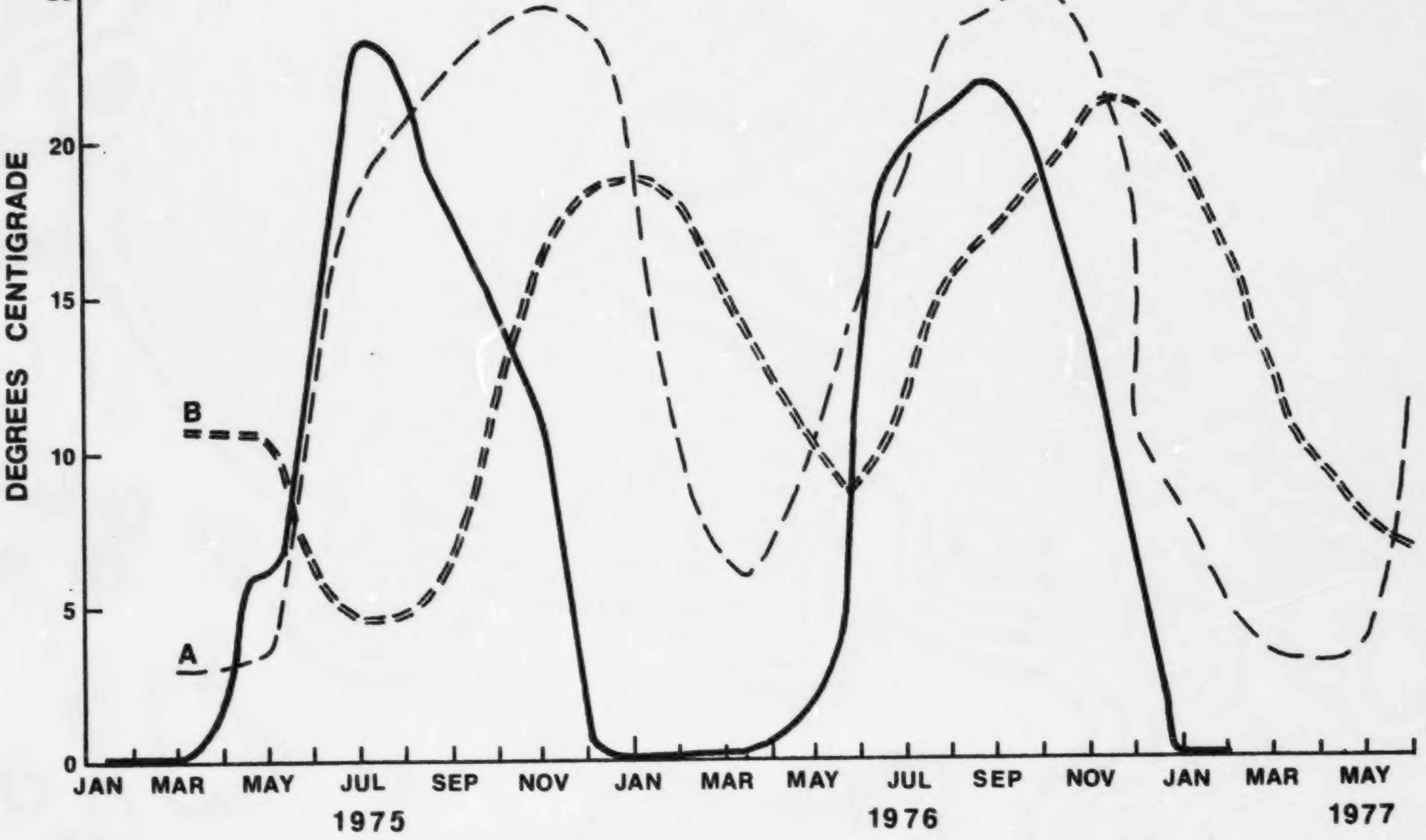

Figure 8. Groundwater temperature variations in wells west of the Columbia cooling pond. Curve A is based on data from a well cased to 4 m below the surface and located 3 m west of the dike. Curve B is based on data from a well cased to 2.5 m below the surface and located 60 m west of the dike. The solid line represents normal seasonal temperature variation in the plant rooting zone for a control site. (Modified from Andrews 1979b).

patterns, surface water flow, and water depth changes are greatest for the area between transects 18 and 30 (Figure 5). This has been designated as the area of major environmental impact for purposes of data analysis. Data were analyzed for this area alone (transects 18 to 30) and for the entire study area (transects 1 to 40). Although the area near the dike between transects 1 and 17 was subject to similar conditions, only two of the six communities occurred in the area. Therefore, transects 1 to 17 were not included in the designated area of major impact.

Plant Community Distribution and Perturbation Patterns

Population and community level responses must be interpreted in light of the intersections of the spatial distribution of plant communities with the different spatial and temporal patterns of perturbation. The plant communities at the Columbia site have not been subjected to the same patterns of perturbation. The type, magnitude, areal extent, and timing of the disturbances were not distributed uniformly either between or within communities. Each plant community occurred at a range of distances from the west dike (Figure 3). Changes in temperature patterns varied as functions of distance from the dike and groundwater discharge patterns. Changes in discharge rates varied according to the distribution of subsurface materials, previous patterns of discharge, and cooling lake temperatures (Andrews 1978b).

Spatial and temporal gradients of environmental change intersected a gradient of wetland community types and resulted in a mosaic of changes in the plant communities. The sequences of change with time differed for each type of disturbance and are not yet complete. Changes in water levels were stabilized by 1975. Temperature changes will not reach equilibrium until some time in the future.

Data sets from two subprojects of the Columbia Study were used to characterize the type, magnitude, areal extent, and timing of disturbance. Data collected by the Hydrogeology Group on groundwater discharge rates, water levels, and groundwater temperatures were the primary sources of information (Andrews 1976, 1978a, 1978b, and 1979; Andrews and Anderson 1978 and 1980; Stephenson and Andrews 1976). Supplementary data from the Wetland Plant Ecology Group on water levels and temperatures of the substrate in the plant rooting zone were used to describe differences between community types. The data set was collected over a greater area of the wetland than the groundwater data. However, a number of caveats must be kept in mind in interpreting the data: 1. The data covered limited periods of time--early summer and mid-fall of each year--and, therefore, do not show important seasonal patterns of change in water depth or temperature. 2. Sample sizes for 1974 (pre-impact) and summer 1975 are small. 3. Temperature data for each community are averaged over areas subject to a gradient of temperature changes and thus mask localized differences. Only substrate temperataures are reported because of high within-sample variability in surface water temperatures attributable to diurnal changes, localized shading or warming effects resulting from the presence or absence of vegetation, or different water depths. 4. Water depth data for each community reflect not only changes in absolute water level, but also changes in depth produced by changes in the elevation and firmness of the peat surface. Groundwater discharging from the cooling lake gradually caused the peat to expand in volume and in some areas caused the layer containing the live roots of plants to detach from the peat mass and float to the surface. The combined effects of high surface water flow, warmer temperatures, and the consequent loss of perennial vegetation caused the peat to decompose and erode in some areas. Thus while water level increased after winter 1975, and depth from water surface to plant rooting zone both increased and decreased between 1975 and 1977. Depth to the top of the plant rooting zone and depth to solid substrate were recorded. Figures 9 and 10 show mean water depth changes for communities within the area of major impact and for the entire study area, respectively. Mean substrate temperatures at the time of vegetation sampling are presented in Figures 11 and 12 for the area of major impact and the entire study area.

Water Level Changes--

Water levels increased and stabilized with respect to mean sea level by 1975 for all communities; levels varied <0.15 m annually after 1975 (Andrews and Anderson 1978). Resulting depth changes in the various communities depended on their respective elevations and drainage characteristics. The meadow/marsh covered a topographic range of 237.26 to 238.20 m; water levels stabilized around 237.96 m. Mean water depth changes and standard deviations for individual communities within the area of major impact are shown in Figure 8. Figure 9 provides similar information for the entire study area. The large standard deviations for all communities are indicative of the varied microtopography and spatial heterogeneity in the wetlands.

According to data collected during the vegetation surveys, depth increases were least in the *CAREX LACUSTRIS* community (Δ cm = +3.6 cm for transects 1 to 40) and greatest in the EMERGENT community (Δ cm = + 24.4 cm for transects 1 to 40). Average increase for all communities was $\underset{\sim}{\sim}$ 10 cm.

By summer 1976 the peat mat had "floated" up in all stations except the *SPIRAEA* and LOWLAND SHRUBS and TREES communities. In most cases this represented an abrupt change from being "non-floating." Thus, after 1975 further changes in water depth shown in the vegetation survey data largely reflect changes in the structure of the peat bed: "floating," decomposition, and erosion.

Temperature Changes--

Localized temperature changes first became evident in early spring 1975, spread gradually, and have not reached equlibrium (Andrews 1978b). Temporal and spatial patterns of change in and between communities are complex. No substrate temperatures were recorded at time of vegetation sampling in summers 1974 and 1975. The spatial distribution of early temperature change must be inferred from other data.

All communities located north of transect 30 and within 125 m of the west dike probably experienced significant temperature changes by December

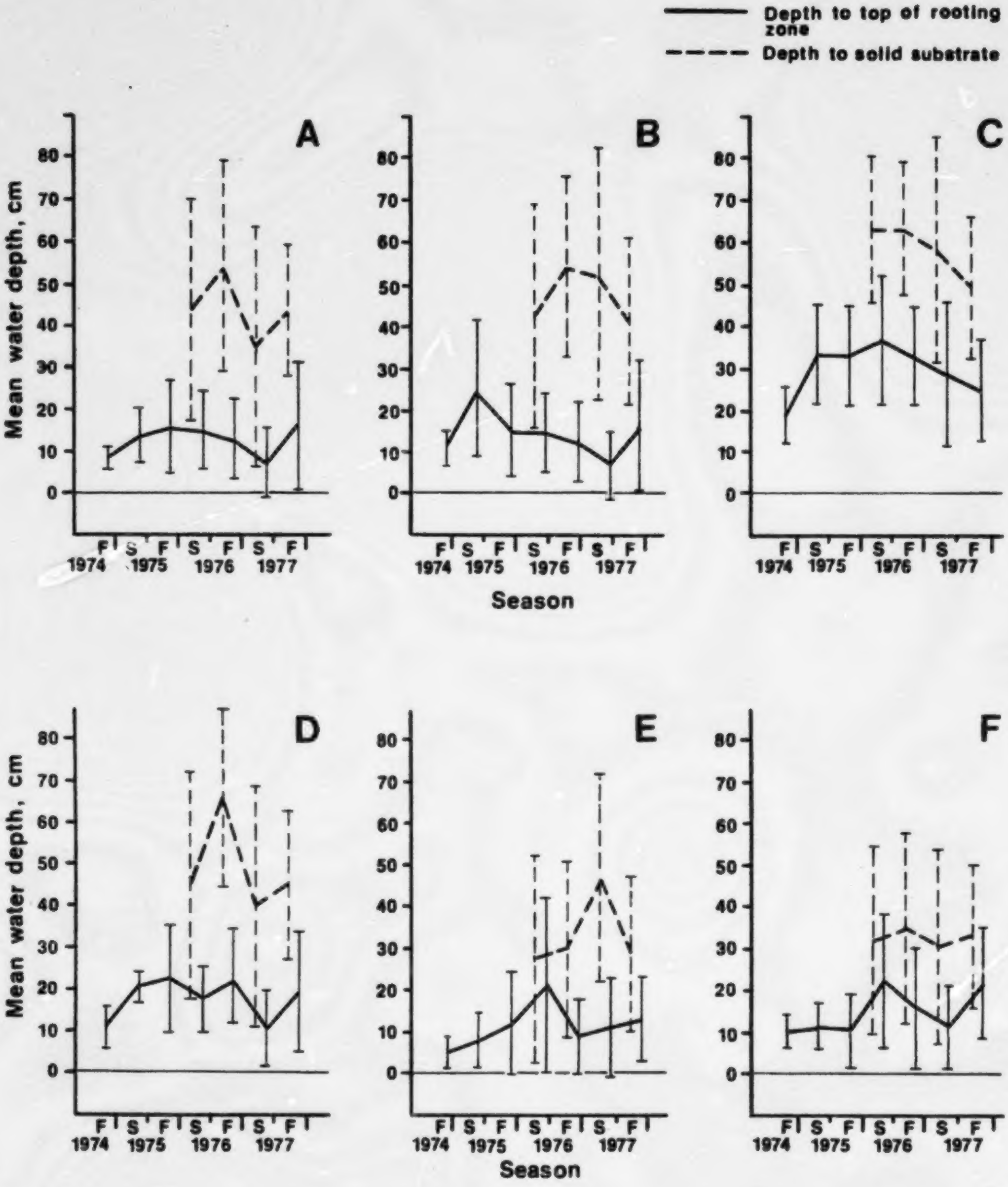

Figure 9. Changes in mean water depth before and after (January 1975) filling of the cooling pond for six wetland plant communities within the area of major impact. Vertical lines indicate ± s.d. of the mean. A is *CAREX LACUSTRIS*, B is *CAREX STRICTA*, C is EMERGENT, D is TRANSITION, E is *SPIRAEA*, and F is LOWLAND SHRUBS AND TREES.

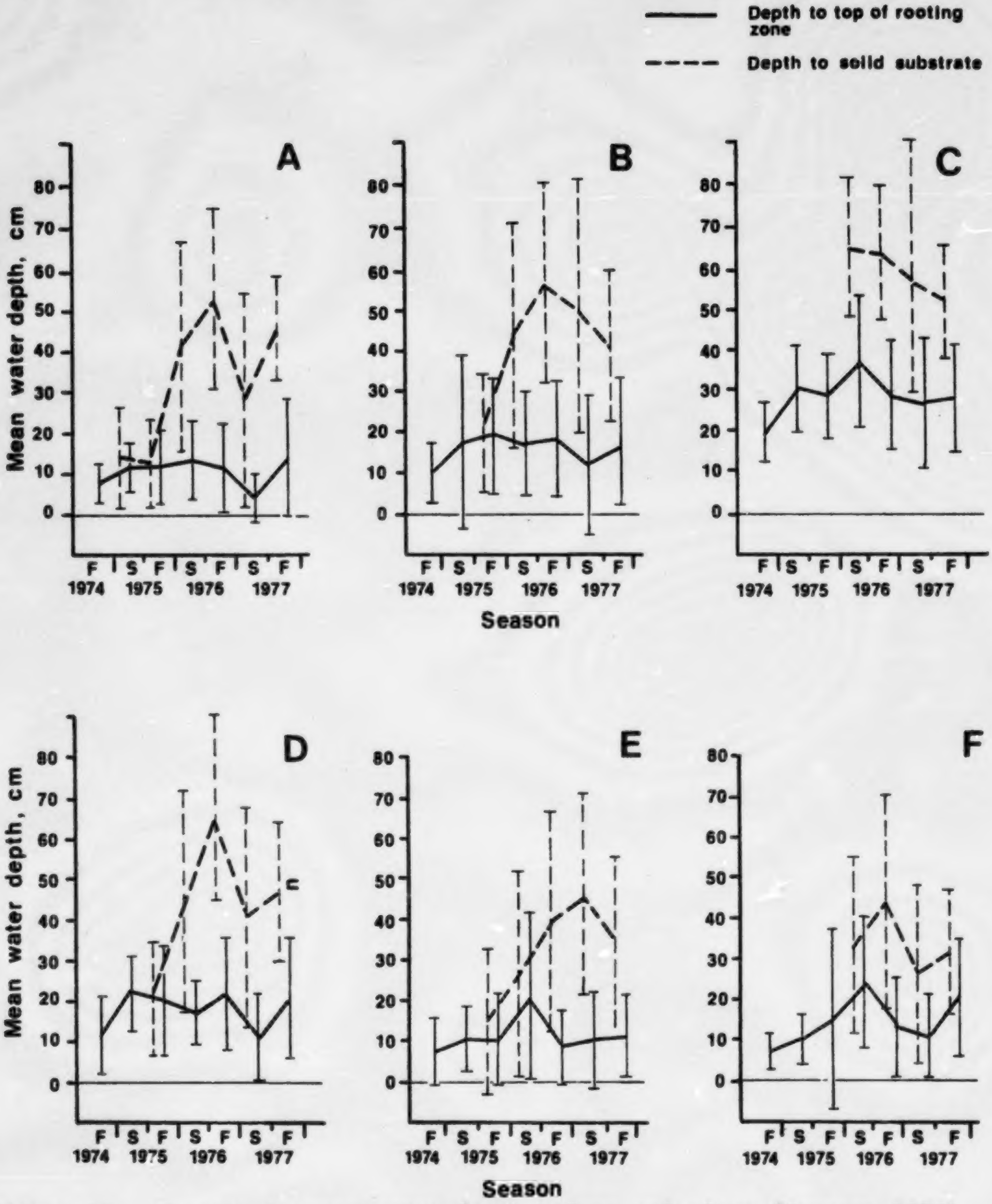

Figure 10. Changes in mean water depth before and after (January 1975) filling of the cooling pond for six wetland plant communities within the entire sampling area. Vertical lines indicate ± s.d. of the mean. A is *CAREX LACUSTRIS*, B is *CAREX STRICTA*, C is EMERGENT, D is TRANSITION, E is *SPIRAEA*, and F is LOWLAND SHRUBS AND TREES.

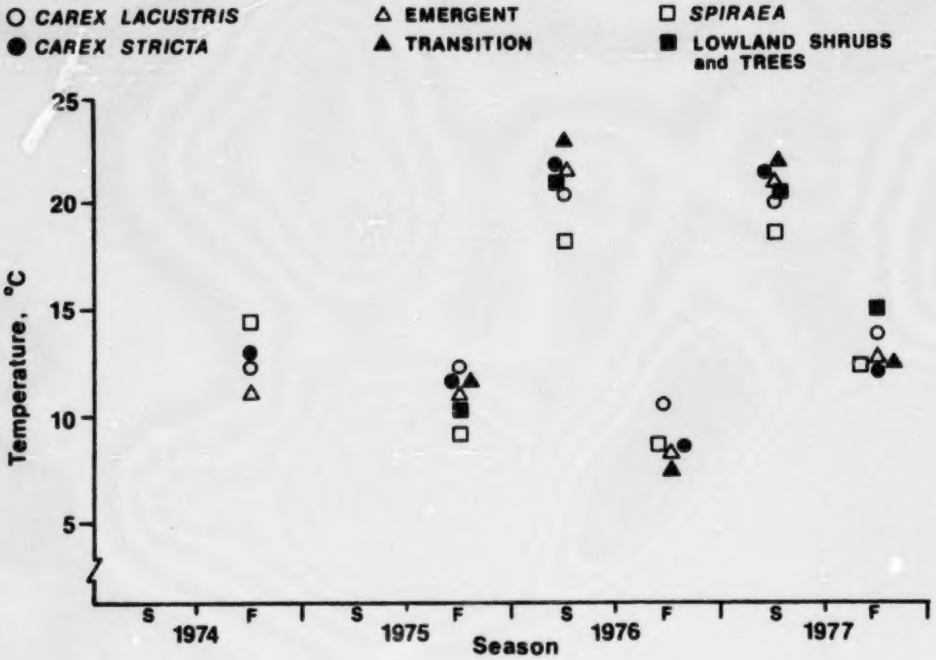

Figure 11. Mean groundwater temperature in the plant rooting zone at the time of vegetation sampling for the area of major impact.

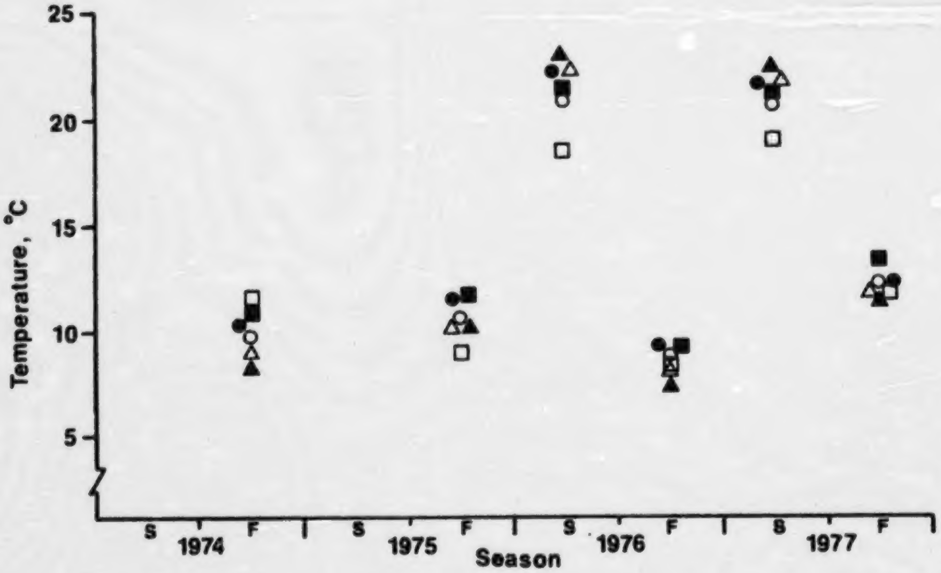

Figure 12. Mean groundwater temperature in the plant rooting zone at the time of vegetation sampling for the entire area.

1975. This conclusion is based on the following information. The Hydrogeology Group first showed localized temperature anomalies in early spring 1975. These anomalies were recorded at 2.1 and 4.6 m below the surface within 95 m of the west dike along transect 8 in the *CAREX STRICTA* community (Stephenson and Andrews 1976). Cold water (<3°C) moving in winter 1975 from the cooling lake, which had been filled between 4 November 1974 and 2 January 1975, discharged in late April 1975 near the west dike where no pronounced low permeability layer occurred beneath the surface. In general, no pronounced permeability layer exists beneath the surface near the west dike north of transect 30. Given this and the fact that "temperatures at a depth of 3 m deviate from those at 0.6 m by less than 1°C" (Andrews 1978b), it is reasonable to assume that changes in seasonal temperature patterns occurred in the plant rooting zone over about 50% of the area of major impact by April 1975. Cold water (< 5°C) discharged in spring, and warm water (16 to 25°C) discharged during late fall and early winter 1975. At $\sim$ 95 m from the dike cold water emerged in mid-summer, and warm water discharged in late fall 1975 and throughout winter and early spring 1976 (Stephenson and Andrews 1976).

The fall of 1975 changes were evident in temperature data taken with the vegetation survey. At that time anomlous temperatures were recorded at 90 out of 291 quadrats sampled for the entire wetland. Most anomalies recorded in fall 1975 were north of transect 30. By summer 1976, temperatures $\geq$ 3°C above control site temperatures were recorded at 192 of 338 quadrats sampled and as far from the dike as 450 m. In fall 1976, anomalous temperatures were $\geq$ 3°C colder than the control temperature at distances > 75 m from the dike or south of transect 30. North of transect 30 temperatures $\geq$ 3°C warmer than the control temperature were recorded 50 to 100 m from the west dike. Summer 1977 patterns were similar to those of summer 1976, with some added data from south of transect 30 indicating that warm water was discharging at 30 of the 36 quadrats sampled between transects 34 and 36. Warmer than normal temperatures also were recorded in fall 1977, but at fewer stations south of transect 30.

The trend appears to be one of gradual warming south of tansect 30. The peat layer near the dike tends to be deeper (Figure 13) and elevations near the dike tend to be higher than elsewhere. Consequently, temperature changes here have been gradual and were at first not very pronounced (Stephenson and Andrews 1976). Localized temperature anomalies were recorded at the time of vegetation sampling as early as fall 1975. However, the anomalous temperatures recorded in fall 1976 south of transect 30 were almost all colder than normal temperatures. By summer 1977, warm temperatures had appeared south of transect 30, as they did in fall 1977 over a somewhat more restricted area.

Spatial and temporal patterns of perturbation are discussed below for each community type within the area of major impact and the entire study area. Each community occurs in both areas. The reader should refer to Figure 3 throughout the discussion.

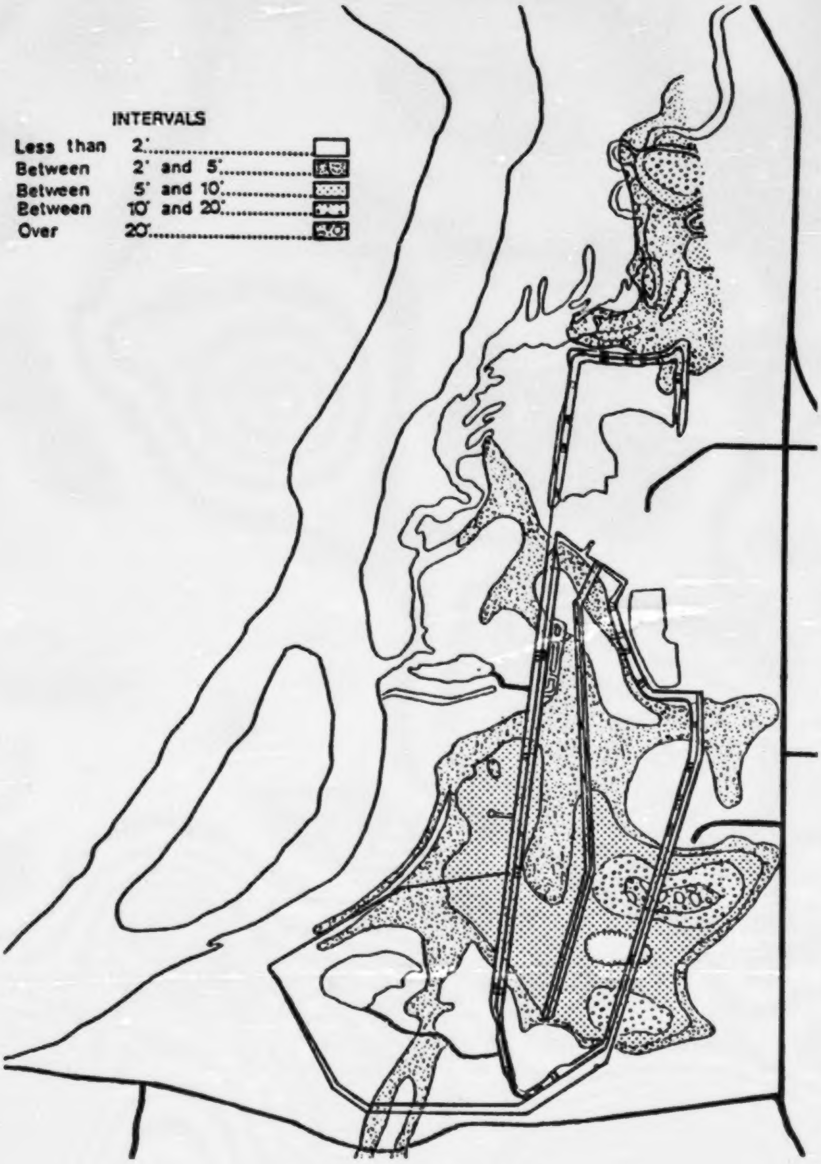
INTERVALS
Less than 2'
Between 2' and 5'
Between 5' and 10'
Between 10' and 20'
Over 20'

Figure 13. Depth of peat and marl deposits at the Columbia site (from Andrews 1976).

CAREX LACUSTRIS Community--

Plant communities within which *C. lacustris* was the most prominent species occupied a major portion of the study area prior to disturbance (Figure 3). Before and after perturbation the *C. lacustris* areas were subject to rates of groundwater discharge higher than areas in which *C. stricta* was more prominent but lower than in areas characterized as TRANSITION and EMERGENT communities (Andrews 1976). As discharge rates increased approximately by a factor of six times, the *CAREX LACUSTRIS* community became subject on the whole to proportionately higher discharge rates. By spring 1976 the increased flow began to cut noticeable channels. Water level increases, however, were minimal for the community as a whole, increasing only from a mean of 8.4 ± 3.8 cm in fall 1974 to 11.6 ± 4.8 cm in 1975.

Within the designated area of major impact (transects 18 to 30), the high surface flow rates resulting from high groundwater discharge within the *CAREX LACUSTRIS* community have kept most of it from freezing since winter 1974 to 1975. Those portions of the community located near the dike (0 to 100 m from the dike) experienced, in addition, the widest range of temperature changes (-4°C to +26°C) and the greatest seasonal displacement of temperature patterns. After 1975, mean substrate temperature in the *CAREX LACUSTRIS* community tended at the time of vegetation sampling to be lower in summer and higher in fall than other communities. Stations located at greater distances were subject to high groundwater discharge but generally lower and somewhat attenuated temperature patterns resulting from longer time lags in movement of water from the cooling lake through subsurface materials and consequently greater dissipation of the heat content of the water.

In general, portions of the community occurring south of transect 30 were located in areas underlain by thicker peat deposits (Figure 13) (Andrews 1976). Discharge rates here, although comparatively higher than in the surrounding *CAREX STRICTA* and *SPIRAEA* communities, presumably were lower than rates north of transect 30. Temperature changes and increases in surface flow rates were consequently more gradual and less pronounced than in the *CAREX LACUSTRIS* community lying north of transect 30. Nonetheless, flow rates were sufficient to cause late freezing and early thawing over much of the area by 1975 to 1976. Altered temperature patterns have increased in areal extent since then.

CAREX STRICTA Community--

Plant communities dominated by the tussocks of *C. stricta* were widely distributed prior to disturbance (Figure 3). They became subject to a wide range of spatial and temporal variation in disturbance patterns depending on factors previously discussed. However, interpretation of results for the *CAREX STRICTA* community differs from that for all other communities, except LOWLAND SHRUBS and TREES. The *CAREX STRICTA* community is the only community with a major proportion of the sampling stations located north of transect 30, within 150 m of the west dike but outside the designated area of major impact, i.e., between transects 1 and 17. This means that for the *CAREX*

STRICTA community, results from the entire sampling area (transects 1 to 40) are influenced strongly by impacts similar to those described previously for transects 18 to 30.

The morphology of *C. stricta* mediated the extent to which plant populations experienced water flow and heat effects. The tops of most tussocks remained elevated above the water, despite the 8 to 10 cm depth increase. This diminished the effects of temperature and surface water flow for plants growing on top of the tussocks. Only plants growing in depressions between tussocks experienced the full effect of change.

EMERGENT Community--

Prior to disturbance the major portion of the EMERGENT community was located in an area of moderate to high groundwater discharge, > 200 m from the west dike and at the lowest range of elevation. Initial water depths ($\bar{X}$ = 16.5 and 20.0 cm for summer and fall, respectively) were greater than for all other communities. In general, the community experienced maximum water level increases (Δ = +24 cm, 1974 to 1975 for transects 1 to 40) and minimal temperature effects. Except for the edge of the community bordering the TRANSITION community where a major flow channel developed, the area remained frozen in winter. Fewer temperature anomalies were recorded here than in the CAREX STRICTA, CAREX LACUSTRIS, or TRANSITION communities. However, the small portion of the community located within the area of major impact and close to the west dike experienced maximum temperature changes and winter open water conditions in addition to a water depth increase of 18.6 cm.

TRANSITION Community--

The TRANSITION community was located in a zone of high groundwater discharge approximately 100 to 250 m from the west dike (Figure 3). Topographically the community was in an area between the SEDGE MEADOW communities and the EMERGENT community. Following perturbation the area became the major channel for surface water movement from the wetland to the Wisconsin River. The high velocity of water moving into and through the area has kept much of the community in open water each winter since 1975. However, tempratures did not change markedly because of attenuation with distance from the dike. Mean temperatures at the time of vegetation sampling tended to be somewhat warmer in summer and somewhat cooler in fall than in other communities, i.e., temperatures were altered slightly but remained in phase with normal temperature patterns. Water levels increased no more than average (Δ = +10.8 cm, 1974 to 1975 for transects 1 to 40).

SPIRAEA Community--

The shrub *S. alba* was prominent in two distinct contiguous zones. The smaller of the two occurred entirely within the area of major impact and probably experienced some departure from normal temperature patterns by spring 1975. Changes were not evident in temperatures recorded at the time of vegetation sampling until summer 1976, likely because of small sample size in 1975 ($n \leq 6$). The larger area of *S. alba* was located south of transect 37, mostly at > 200 m from the west dike. Temperature changes here were minimal.

Changes in water flow were negligible for each area. Both were snow covered through the winters 1974 to 1975, 1975 to 1976, and 1976 to 1977. However, it is reasonable to assume that the substrate within the area of major impact did not remain frozen throughout the winters 1975 to 1976 and 1976 to 1977.

Because *S. alba* tended to occur on slightly elevated "islands" in the meadow/marsh, it is assumed that water level increases were minimal. However, 1974 data do not provide a large enough sample to say definitely what water levels in the *SPIRAEA* community had been. Field observations made in 1974 indicate that the community usually had no water standing above the surface after June before leakage from the cooling lake changed discharge patterns in 1975. Since that time water has been ≥ 10 cm deep.

LOWLAND SHRUBS and TREES Community--

Areas dominated by a mix of lowland shrubs and trees also tended to occur on somewhat elevated "islands" or "ridges" in the meadow/marsh. Although data is minimal for 1974, it is reasonable to assume that this community rarely had standing water except at times of flooding. Since 1975, average water depth at time of vegetation sampling was ≥ 10 cm. Surface water flow tends to move around these areas and the community freezes at least at the surface in winter. Temperature changes--as with other communities--have been most pronounced in portions of the community located near the dike.

Plant Populations and Community Responses

Vegetation response associated with leakage of water from the cooling lake was rapid. Significant departures from normal shoot emergence patterns and extensive mortality of dominant perennial species occurred within 1 yr of station operation. Rapid invasion of newly opened habitat by annuals and the spread of tolerant, more hydrophytic perennial species followed. Entire populations of plants were depleted and replaced by other species. Some areas remain completely unvegetated. Species diversity and equitability decreased overall in spite of increases in species number.

In general, effects on the vegetation occurred first in the area between transects 18 and 30 where proximity to the cooling lake and high groundwater flow rates coincided. Trends observed here spread to other areas of the wetland by 1977 and indicate the probable response pattern for the entire wetland given predicted, long-term thermal alterations (Andrews 1978b). Field observations and sampling data are used below to describe and quantify the patterns of population responses and community dynamics from 1974 through 1977.

Field Observations of Phenological Change--

Notable departures from normal patterns of shoot emergence and growth first occurred in October 1975, ∿6 months after the Columbia station began operation. At that time, unusually late growth and flowering of *S. latifolia* and *T. latifolia* were noted in localized areas within 25 m of the cooling lake's west dike. Color infrared aerial photographs taken on 5 November 1975 indicated active photosynthesis by *L. minor* up to 200 m away from the west dike (Wynn 1979).

Plant mortality and altered shoot emergence patterns were extensive and obvious by spring 1976 within 200 m of the dike between transects 18 and 30. A large proportion of the area, which previously was densely vegetated, contained only sparsely scattered live shoots of perennial plants by late May. Areas of *C. lacustris* with dense standing dead material showed no live shoots or only stunted, sparsely scattered clumps. Entire areas of overwintering and spring emergent shoots of *C. rostrata* died back by June. *T. latifolia* shoots failed to emerge or emerged late. Numerous forbs (*Mentha arvensis, Lysimachia thyrsiflora*, and *Potentilla palustris*) emerged, but their growth was stunted. Some localized mortality of *Carex lasiocarpa* and *C. canadensis* also was noted, as was chlorosis and/or poor growth for many species.

Fall 1976 shoot emergence and senescence patterns also changed. *S. latifolia, T. latifolia,* and *C. stricta* remained green into late October. Fall-emerging shoots of *C. lacustris* were reduced in number but were taller than normal over-wintering shoots. Shoots of *T. latifolia*, which normally are formed in the fall but do not emerge until spring, emerged throughout the fall and into the winter within 50 m of the dike. Most of the emergent shoots were chlorotic and did not exceed 60 cm in height.

By 1977 similar patterns of altered phenology and extensive plant mortality were evident within 150 m of the dike through much of the entire study area (transects 1 to 40). The phenological changes evident in spring and fall revealed trends of change in the vegetation otherwise obscured by apparently "healthy" summer growth. Individual responses signaled population responses.

Population Responses to Perturbation--

Species response to impact varied according to three factors: 1. Life history characteristics of the species, 2. the location of the species in the marsh relative to areas of major water temperature changes and increased groundwater discharge from the cooling lake, and 3. the community type in which the species occurred. The population responses of 12 abundant species are discussed for the area of major impact (transects 18 to 30) and the entire meadow/marsh.

The average number of shoots per quadrat is used as an indicator of species response. Summer or fall data are given in the figures, depending on the phenology of the species under consideration. In general, the sampling date that expressed the maximum shoot density of the species, e.g., after shoot emergence or before senescence, is discussed.

Responses in the area of major impact--The five species--*C. lacustris, C. stricta, C. rostrata, C. canadensis,* and *T. latifolia*--are relatively long-lived, rhizomatous perennials. *T. latifolia* generally tolerates deeper water than the other four species. It often occurs in dense monotypic stands, and reproduces vigorously by both vegetative spreading (Fiala 1971) and by seeds. It generally grows to a greater height than the other four species. *C. lacustris* and *C. rostrata* are both found at intermediate water depths and may form relatively dense, even stands by producing new shoots from buried rhizomes (Bernard 1975 and 1976). *C. stricta* differs from the two previous sedges in its tussock growth habit (Costello 1936). The tussocks, formed of tough, fibrous roots and rhizomes, generally elevate the shoot bases above the water surface. *C. canadensis* has a relatively fine, but equally fibrous, root system compared to the sedges and appears to be best adapted to continually damp but not saturated soil conditions (Mueller-Dombois and Sims 1966). It sometimes occurs as a co-dominant with *C. stricta* in Wisconsin marshes, growing between the tussocks (Stout 1912, Costello 1936). Costello (1936) found that *C. canadensis* was an important competitor with *C. stricta*, generally outcompeting the tussock sedge in the drier portions of sedge meadows. However, Stout (1912), in a study of a wet meadow in Dane County, Wis., found that *C. canadensis* exceeded *C. stricta* in density and dry weight in the wettest part of the sedge meadow, while *C. stricta* was dominant in somewhat drier portions. The reason for these contradictory results is not clear but may relate to fluctuating water depths rather than average water depths.

Of these five long-lived, rhizomatous species only *T. latifolia* exhibited a consistent increase in shoot density in the area of major impact between 1974 and 1977 (Figure 14). *T. latifolia* was present in measurable numbers in only the EMERGENT community in 1974. By 1977, its shoot density had increased more than three-fold in that community. In addition, in 1976 and 1977, *T. latifolia* appeared in low densities in the TRANSITION community, indicating it may have been increasing in area and density after impact.

In sharp contrast to the response of *T. latifolia, C. lacustris* and *C. rostrata* declined in shoot density in all communities between 1974 and 1977 (Figure 15, Figure 16). In the *CAREX LACUSTRIS* community, *C. lacustris* dropped in shoot density from 12.6 stems/quadrat in 1974 to 2.8 stems/quadrat in 1977. In the four other community types, *C. lacustris* shoot density fell to < 1 stem/quadrat (Figure 15).

C. rostrata, present in fewer communities in 1974 than *C. lacustris*, showed a similar response pattern (Figure 16). In the TRANSITION community, where *C. rostrata* reached its highest initial density (∿ 7.8 stems/quadrat), it was virtually eliminated by 1977. It also appeared to be eliminated from the *SPIRAEA* and *CAREX LACUSTRIS* communities. However, by 1977 in the EMERGENT community, *C. rostrata* was still present at > 50% of its original shoot density, despite a sharp decline in 1975. The greater average distance of the EMERGENT community from the west dike may account for this response.

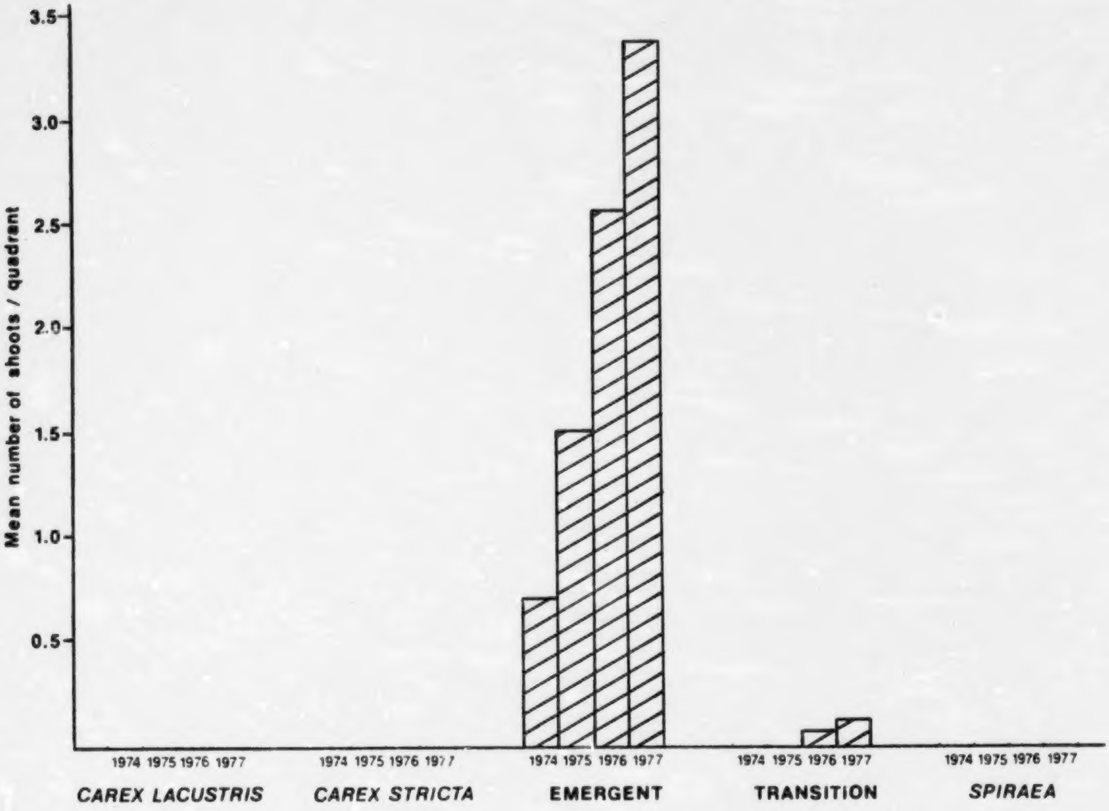

Figure 14. *Typha latifolia*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) in five wetland plant communities in the area of major impact.

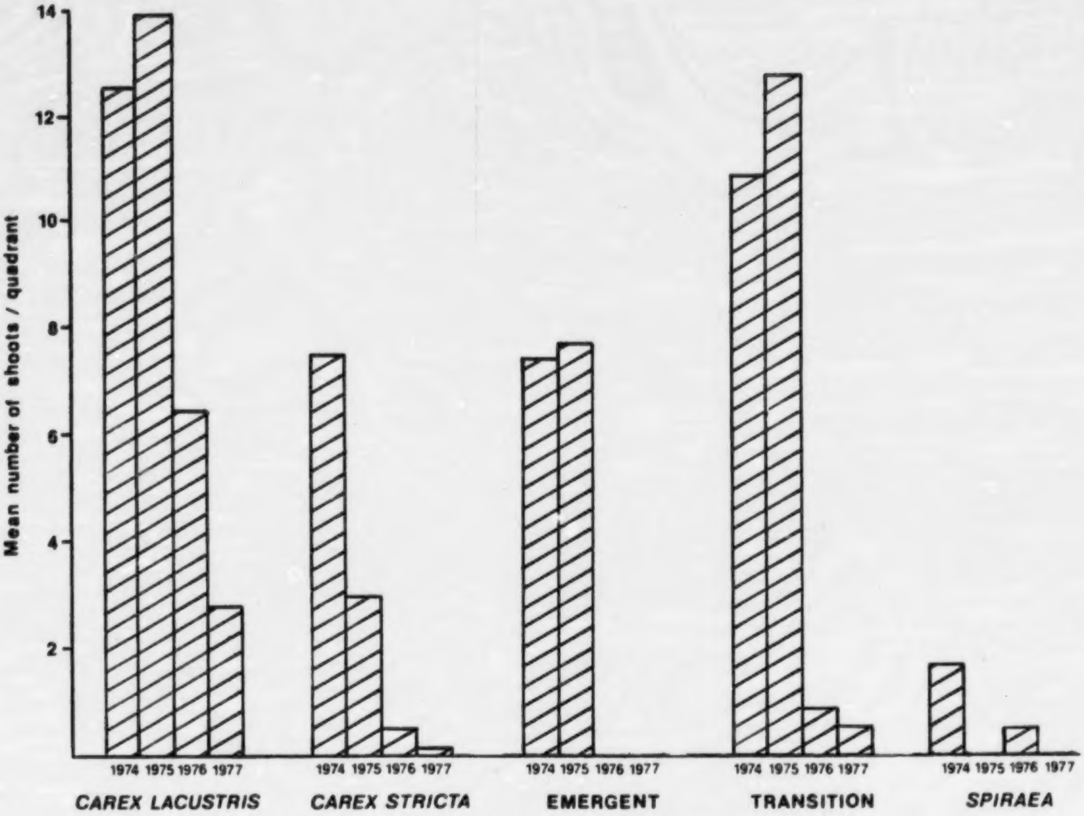

Figure 15. *Carex lacustris*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities in the area of major impact.

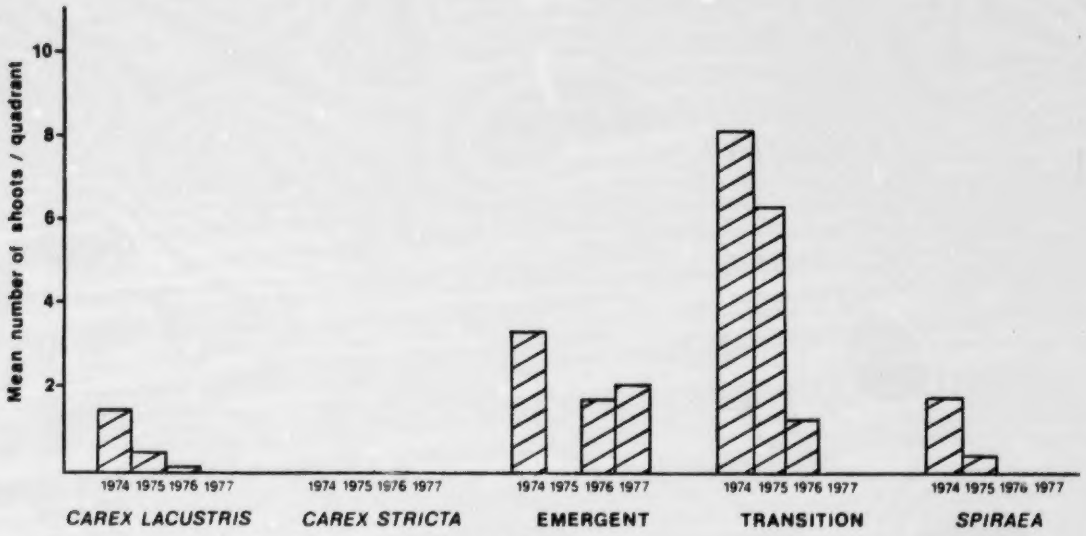

Figure 16. *Carex rostrata.* Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities in the area of major impact.

C. stricta and *C. canadensis* exhibited remarkably similar trends in shoot density over the 4-yr period (Figure 17, Figure 18). In general, the shoot density of both species increased in 1975 and 1976, and declined sharply in 1977, except in the *SPIRAEA* community where both species sustained an increase in shoot density through 1977.

A change of some interest, which is not evident from Figure 17 and Figure 18, is the change in summer:fall shoot density ratios between 1974 and 1977 for *C. stricta* and *C. canadensis*. In 1974 for *C. canadensis*, and in 1975 and 1976 for *C. stricta* and *C. canadensis*, the fall shoot density exceeded the summer shoot density in all communities with three exceptions (*C. canadensis*, *SPIRAEA* community, and 1976, EMERGENT community; *C. stricta* 1976, *SPIRAEA* community). The average summer:fall shoot ratios for *C. canadensis* for 1974, 1975, and 1976 were 0.35, 0.46, and 0.86, respectively. In 1977, the summer:fall shoot ratio switched to 1.94. For *C. stricta*, the 1975 and 1976 summer:fall shoot ratios were 0.33 and 0.80, respectively. By 1977, the ratio was 1.19. In 1977, the summer shoot density exceeded the fall shoot density in four of five communities for the two species. The exception was the TRANSITION community for *C. stricta* and the *SPIRAEA* community for *C. canadensis*.

The perennial species--*Sagittaria latifolia* and *Epilobium coloratum*--are short-or medium-lived. *S. latifolia* is a short-lived, broad-leaved perennial usually occurring in somewhat deeper water than *C. stricta*. It forms a long, open system of rhizomes, rather than a dense mat, and as a result is usually a weak competitor compared to the preceding sedge species and *T. latifolia* (Costello 1936). However, Sculthorpe (1967) noted *Sagittaria's* ability to spread rapidly within a growing season into unoccupied areas. *E. coloratum* is a medium-lived, erect, bushy perennial. It has fibrous roots and very short rhizomes (Gleason and Cronquist 1963) and occurs on saturated, exposed peat or muck surfaces.

S. latifolia exhibited a mixed response to impact, increasing in shoot density in some communities, while decreasing in others (Figure 19). By 1977, *S. latifolia* shoot density increased by 127% in the TRANSITION community and by 243% in the *CAREX LACUSTRIS* community. It decreased by < 50% in the *CAREX STRICTA* and EMERGENT communities, but seemed to be virtually eliminated from the *SPIRAEA* community.

The mixed response and the particular community types in which *S. latifolia* increased and decreased suggest that its responses may reflect competitive effects rather than the direct effects of high water levels and increased water temperatures and flow. *Sagittaria* increased in the two communities whereas *C. lacustris*--originally a strongly dominant species--declined severely in 1976 and 1977. *Sagittaria* decreased somewhat in the EMERGENT community where *T. latifolia* showed a marked increase in shoot density, and in the *SPIRAEA* community where *C. stricta* and *C. canadensis* increased in density. In the *CAREX STRICTA* community, *Sagittaria* also declined somewhat even though both *C. canadensis* and *C. stricta* showed a net decline. However, the two latter species increased in density in this community through 1976, showing a net decrease only in 1977, and probably largely prevented an increase in *Sagittaria* until that time.

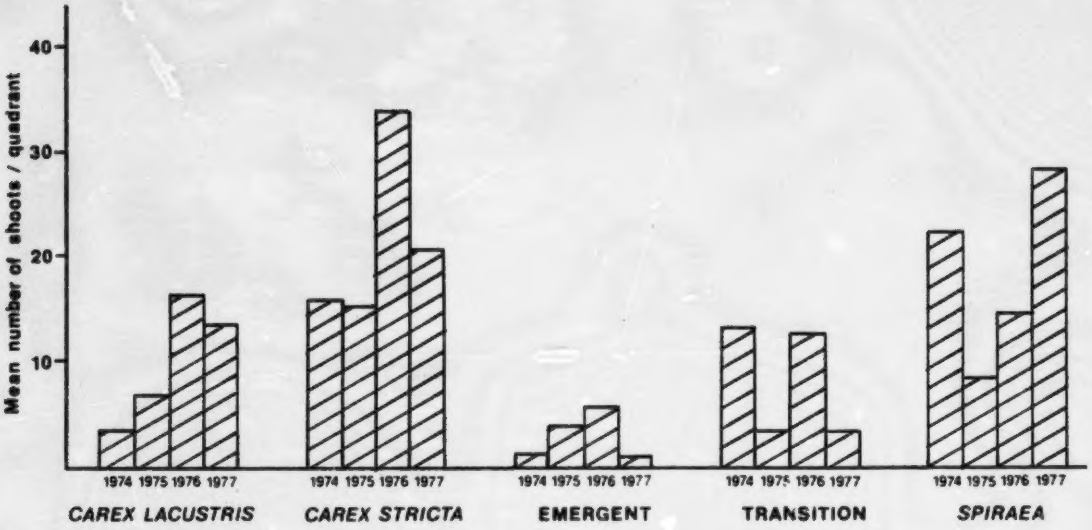

Figure 17. *Carex stricta*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities in the area of major impact.

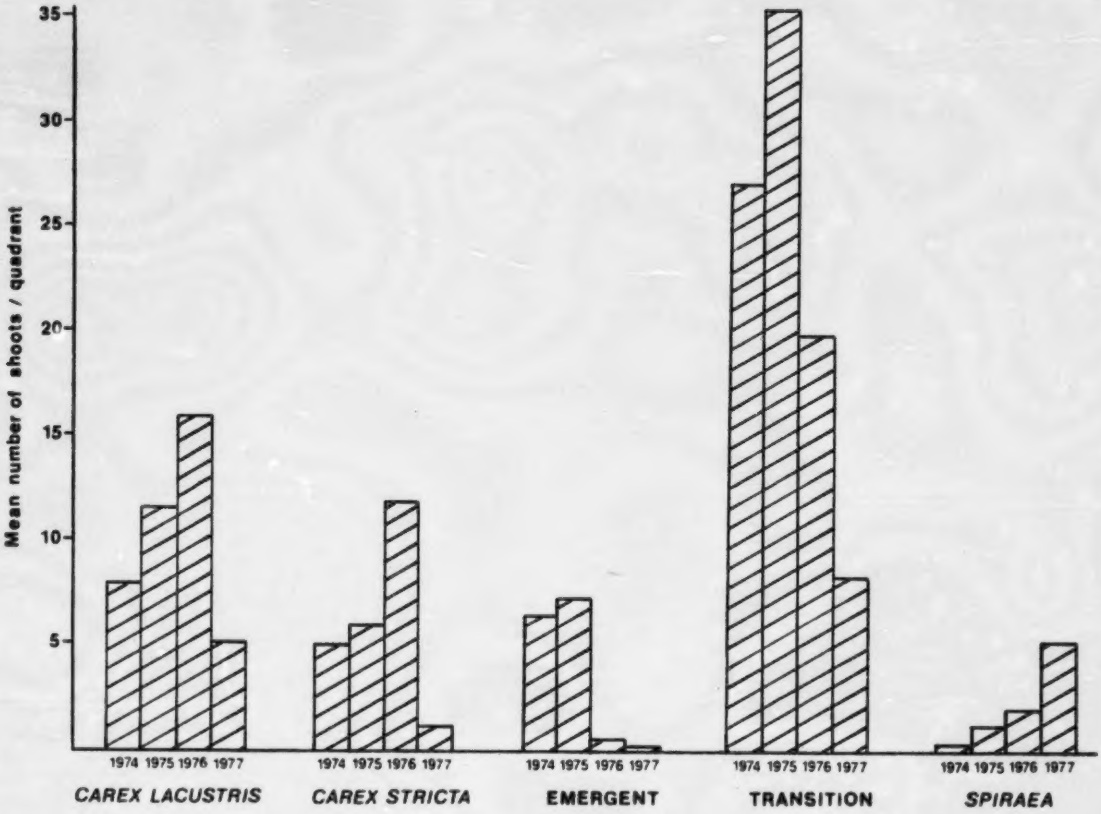

Figure 18. *Calamagrostis canadensis*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities for the area of major impact.

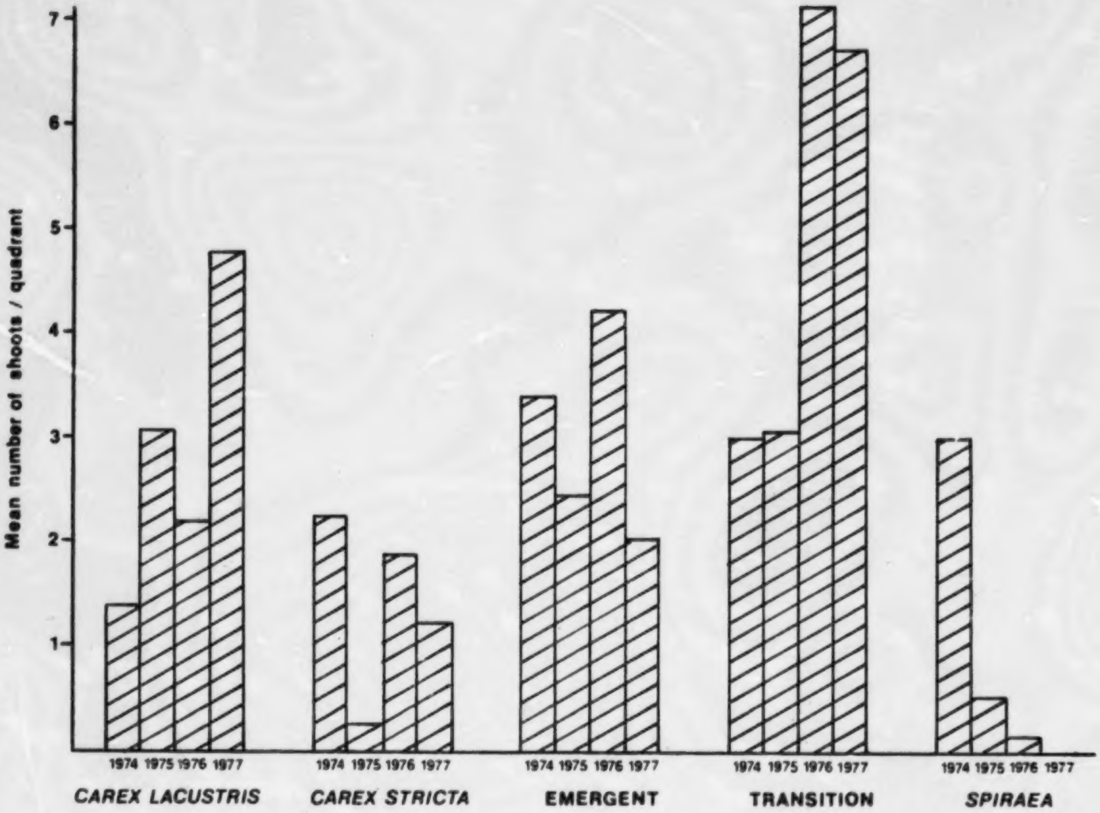

Figure 19. *Sagittaria latifolia.* Changes from summer 1974 to summer 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities in the area of major impact.

The response of *E. coloratum* is shown in Figure 20. Throughout most of the meadow/marsh complex, *E. coloratum* was rare or only occasionally present in 1974 and 1975. Prior to impact, it was represented best in the *SPIRAEA* community on sites slightly elevated and drier than other portions of the marsh. By 1977, in the *SPIRAEA* and *CAREX LACUSTRIS* communities, *E. coloratum* increased from a relatively minor species to an average shoot density of $\underset{\sim}{\sim}$ 4 stems/quadrat. Its increase in the *CAREX LACUSTRIS* community probably results from a decrease in the *C. lacustris* population, combined with exposed floating portions of the peat mat, which together provided open space suitable for colonization by *E. coloratum* seeds. The observed increase in the *SPIRAEA* community may be due to increased light availability on peat exposed below dying *Spiraea* shrubs.

The annual species--*Bidens cernua* and *Pilea pumila*--are capable of proliferating rapidly by seed in the meadow/marsh environment. However, they differ in germination and light requirements. *P. pumila* is a thin-stemmed, often delicate, shade-tolerant species. It is often found as a dense group of small plants on the tops of *C. stricta* tussocks, overtopped and shaded by the stems and leaves of the sedge. *P. pumila* appears to germinate well under cool, moist conditions.

In contrast, *B. cernua* requires an open, sunny site and high soil temperatures for seed germination, such as is found on exposed mud flats and floating peat. *B. cernua* is a tall, coarse-branched plant that often overtops the sedges in the fall after they have begun to brown.

In 1974, *Pilea* was present in moderate densities (3 to 12 stems/quadrat) in three of the five community types; it was rare or absent in the other two. By 1977, its shoot density increased dramatically in the three communities where it was originally present in moderate numbers. *Pilea* reached a remarkably high density of 144 stems/quadrat in the *SPIRAEA* community in 1977 (Figure 21).

Prior to impact, *B. cernua* was not present in measurable numbers in any of the five communities (Figure 22). In 1976 and 1977, *B. cernua* shoot density increased suddenly in the *CAREX LACUSTRIS* and *CAREX STRICTA* communities from near 0 to $\underset{\sim}{\sim}$ 5 and 13 stems/quadrat, respectively. In the *SPIRAEA* community, a smaller increase was noted for 1976 and 1977. Low densities of *B. cernua* also were noted in the TRANSITION and EMERGENT communities by 1977.

Although these two annual species differ markedly in germination and light requirements, locally large increases in shoot density in both species were measured. This indicates that the impact of water level, flow, and temperature changes in the area of major impact has been severe enough to create opportunities for colonization and invasion by annuals, as well as seed-dispersed perennials, like *E. coloratum*, in a previously closed, mature community. The responses of these three species, along with other indicator species such as *L. minor* (discussed later), can be used to characterize the magnitude of the changes in physical and vegetational aspects of the meadow/marsh.

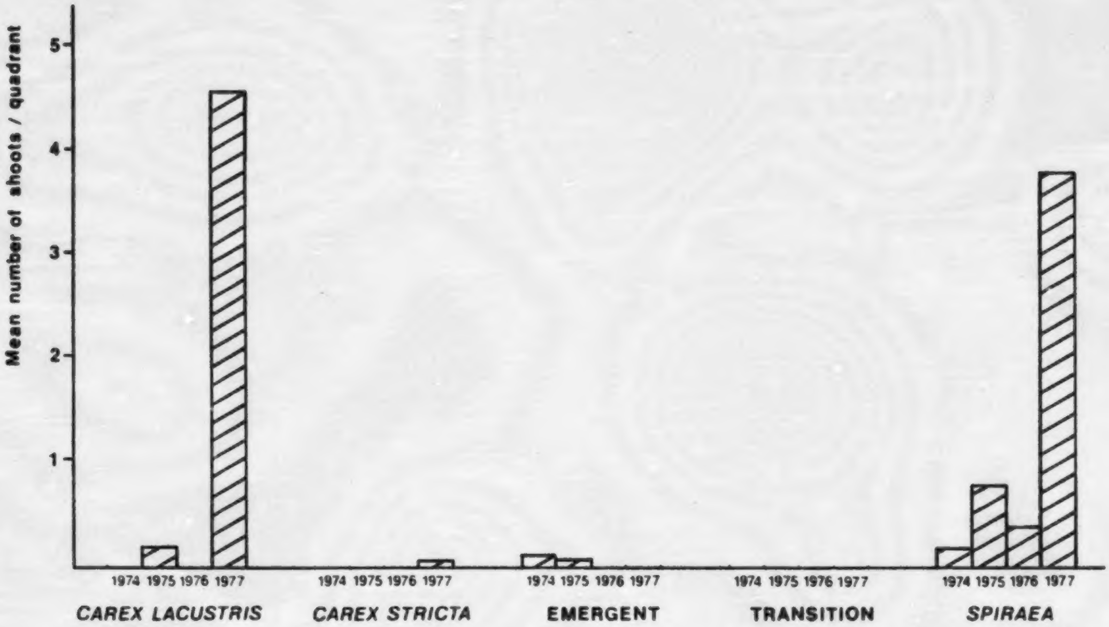

Figure 20. *Epilobium coloratum*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities in the area of major impact.

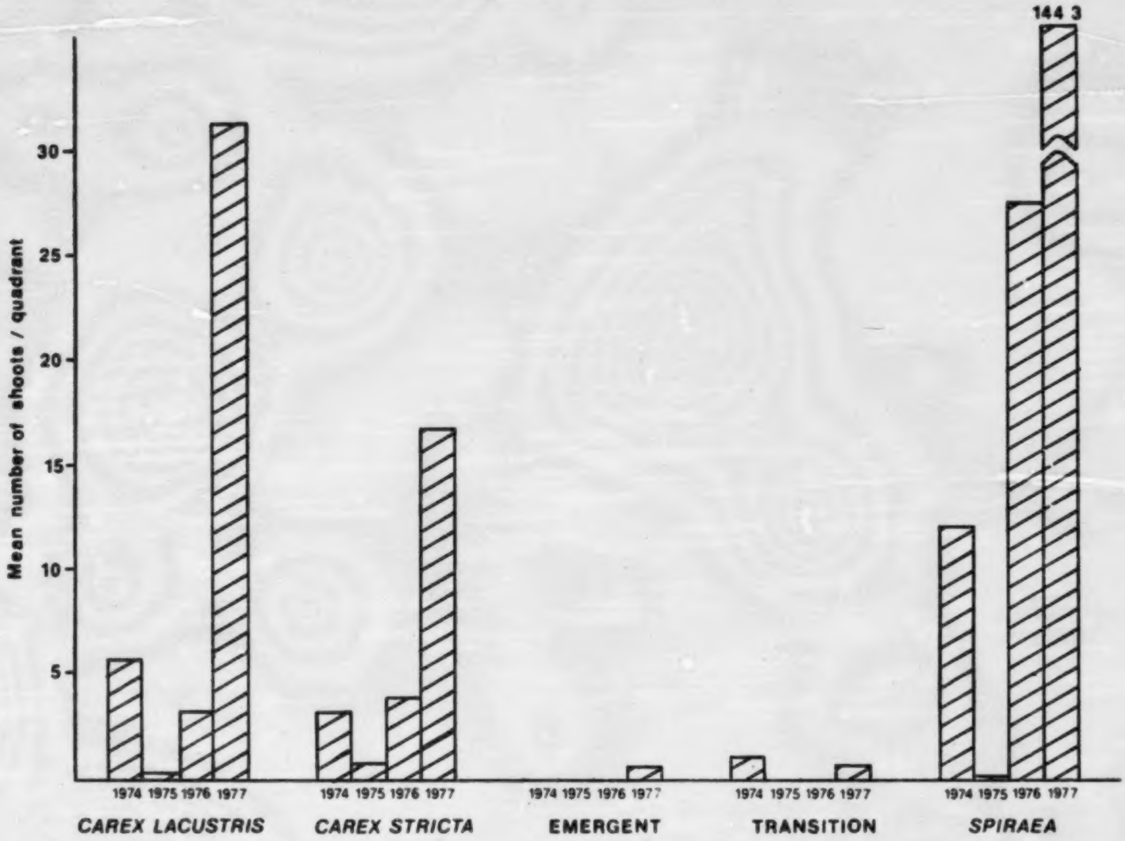

Figure 21. *Pilea pumila.* Changes from summer 1974 to summer 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities in the area of major impact.

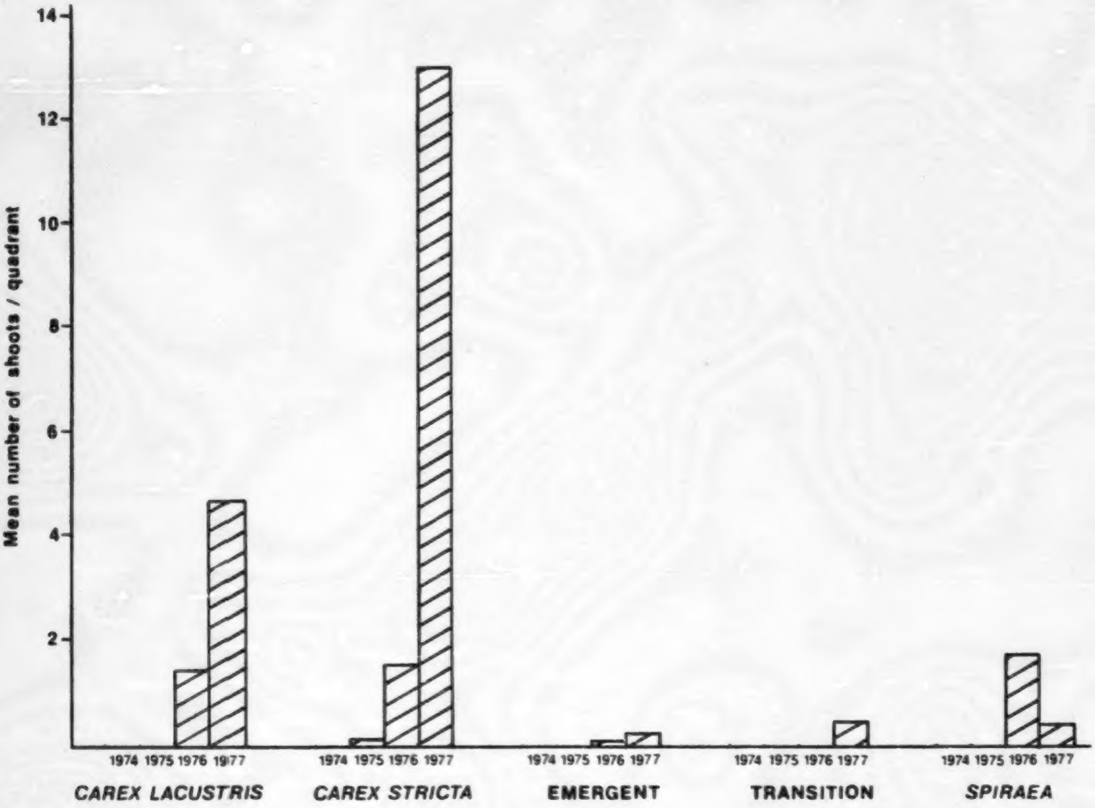

Figure 22. *Bidens cernua*. Changes from summer 1974 to summer 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities in the area of major impact.

Responses over entire marsh—Data for species responses over the entire marsh (transects 1 to 40) average information from the severely- and less-impacted areas of the marsh. Thus, for most species, population changes between 1974 and 1977 in the whole marsh show similar, but less pronounced, trends in shoot density than the area of major impact. However, in some cases, somewhat different trends are apparent in data for the entire sampling area. For certain species--*S. eurycarpum* and *S. alba*--the major portion of the population was located originally almost entirely outside transects 18 to 30. For these species, particularly *S. eurycarpum*, the data from the entire area are especially informative.

Of the long-lived *Carex* spp., *Carex rostrata* formed a disproportionately large part of the total population in communities outside transects 18 to 30 prior to impact. In 1974, the average shoot density of *C. rostrata* in the TRANSITION and EMERGENT communities was 2 to 4 times greater for the whole marsh than for transects 18 to 30 (Figure 23). However, the final shoot densities of *C. rostrata* for the whole marsh data in 1977 were nearly as low as those recorded in the area of major impact. Thus, for *C. rostrata*, the decline in shoot density averaged over the whole marsh was as great or greater than the decline observed in transects 18 to 30.

Carex stricta also showed somewhat different trends between the two data sets. Shoot density of *C. stricta* averaged over the whole marsh (Figure 24) in 1974 was substantially higher in at least two communities than in the corresponding community types in transects 18 to 30. In the *CAREX STRICTA* community, shoot density for the whole marsh was 100% higher than in transects 18 to 30, while in the *CAREX LACUSTRIS* community, shoot density was > 70 stems/quadrat for the whole marsh compared to 3 stems/quadrat in the area of major impact. These high 1974 values for the whole marsh, when compared to 1977 values, indicate net decrease in shoot density of *C. stricta* in two communities, namely, *CAREX LACUSTRIS* and *CAREX STRICTA* types. This is a reversal of the trends shown for *C. stricta* in these two communities in the area of major impact (Figure 17). In addition, *C. stricta* remained at $\underset{\sim}{\ }$ 10 stems/quadrat in the TRANSITION community from 1974 to 1977 in the whole marsh data, rather than decreasing as shown for transects 18 to 30. The variability may reflect the comparatively small sample size in transects 18 to 30 for 1974 and 1975 (n = 8).

In contrast to the preceding two sedge species, *C. lacustris* shoot density did not differ markedly between the area of major impact and the whole marsh (Figure 25). As expected, the only noticeable difference is that *C. lacustris* shoot density does not drop quite as low in the whole marsh as it does in the area of major impact, e.g., it remains slightly > 1 stem/quadrat instead of being virtually eliminated.

For the whole marsh, *T. latifolia* responded in a manner similar to that of the major impact area (Figure 26). Shoot density was marginally lower in the whole marsh, and the increase for each successive year after impact was lower compared to that shown in Figure 14. That is, general trends were the same but lagged each other in time.

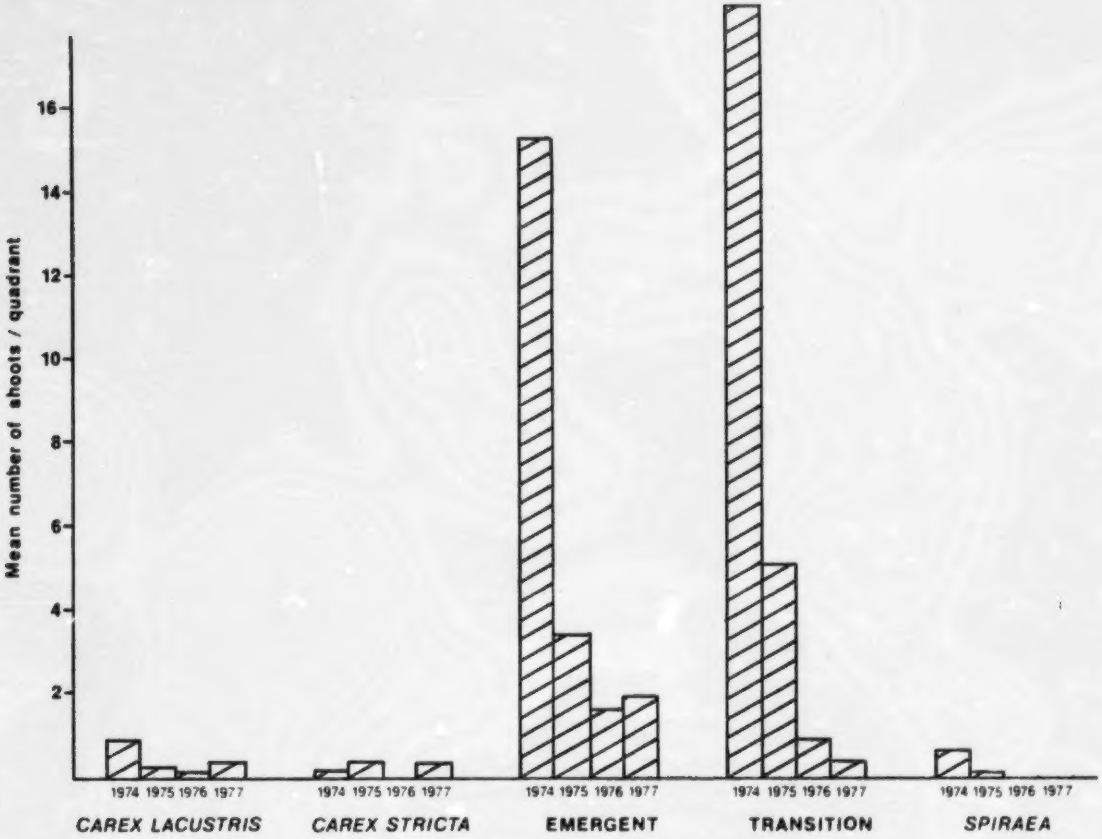

Figure 23. *Carex rostrata.* Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities for the entire sampling area.

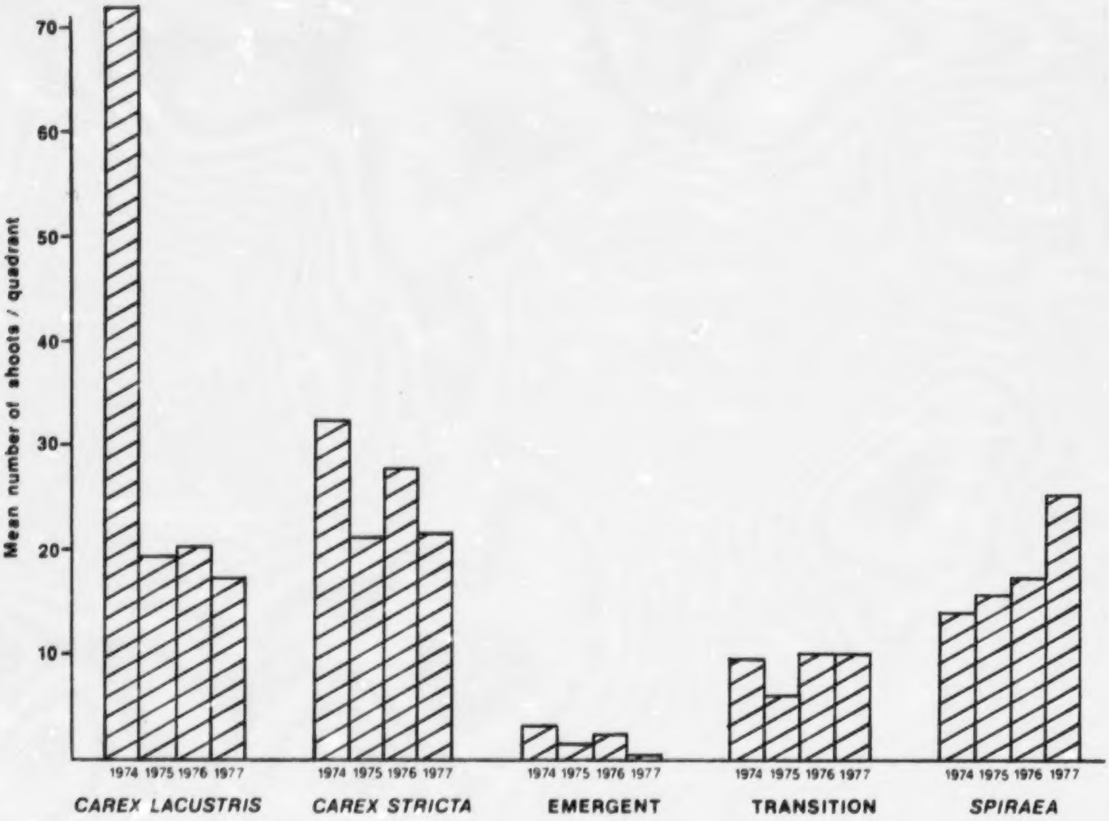

Figure 24. *Carex stricta.* Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities for the entire sampling area.

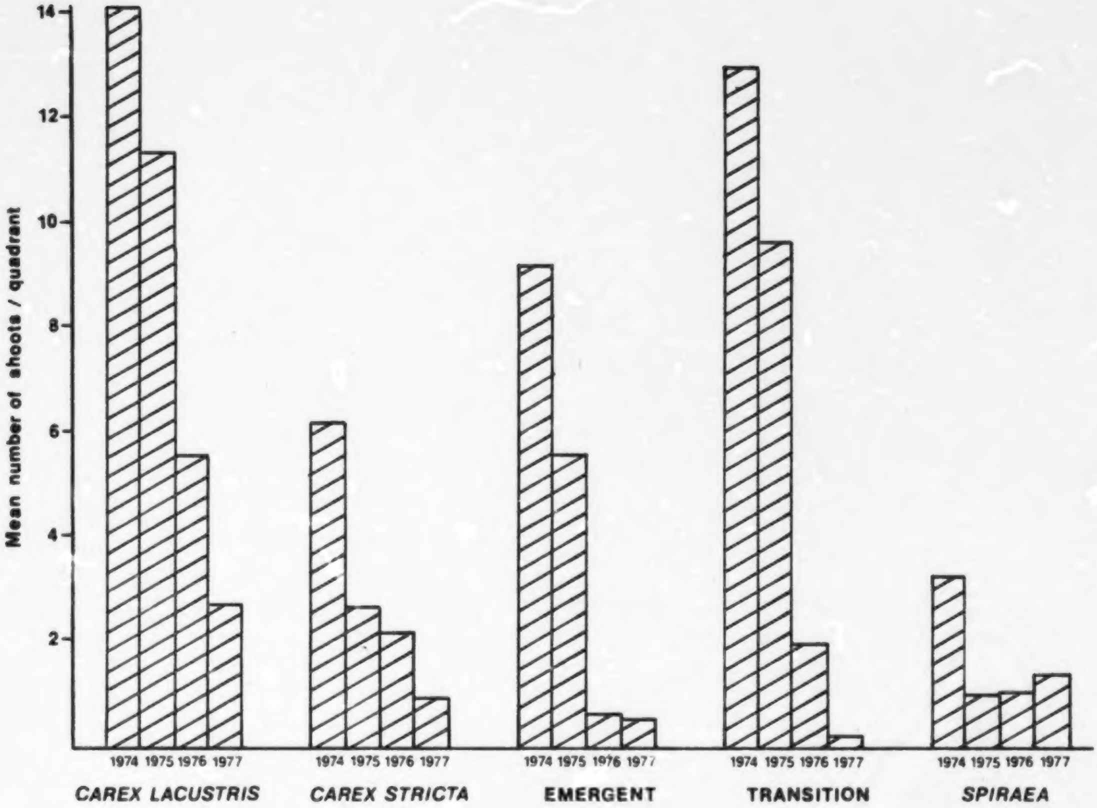

Figure 25. *Carex lacustris*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities for the entire sampling area.

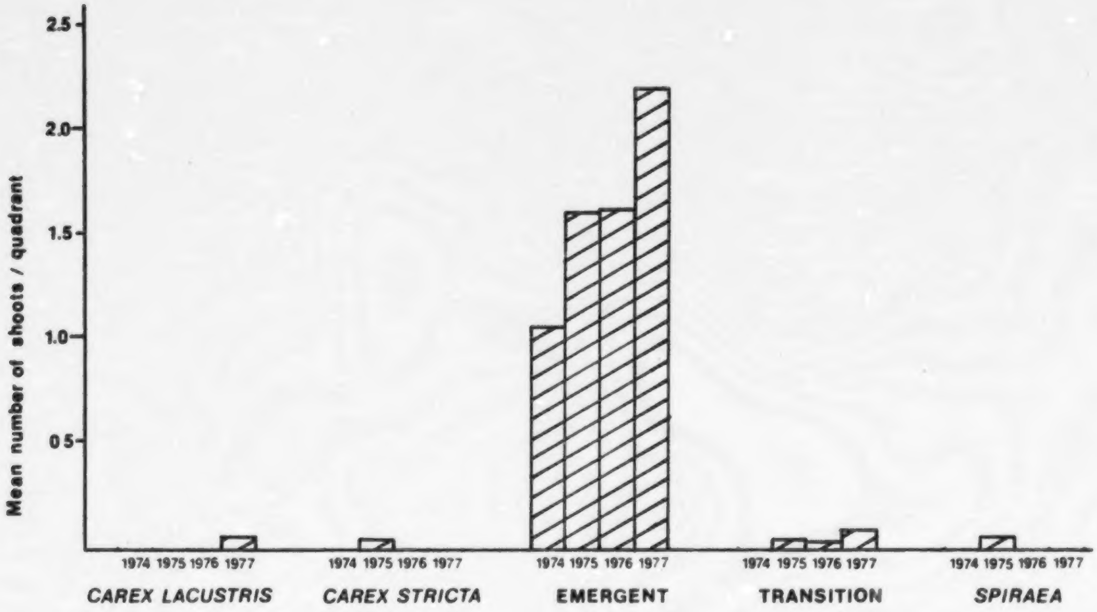

Figure 26. *Typha latifolia*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities for the entire sampling area.

The response of *C. canadensis* differed only slightly for the two data sets. The overall shoot density in the whole marsh (Figure 27) generally fluctuated less than in the area of major impact for all years. This is likely a function of smaller sample size for transects 18 to 30.

Of the medium- or short-lived perennials, *E. coloratum* responded in the same manner in the entire marsh as it did in the area of major impact. However, as expected for an invading species, shoot densities were slightly higher in the area of major impact.

S. eurycarpum is a deep water emergent species. It often occurs with *T. latifolia* but in less dense stands. Because of its tolerance of deep water, *Sparganium* might be expected to be favored over the sedges with an increase in water depth. However, it is not aggressive enough to compete well with the densely growing and rapidly spreading *T. latifolia*.

Although *Sparganium* did occur locally in the area of major impact, a disproportionately large part of the population occurred outside transects 18 to 30. Prior to disturbance, it was confined largely to two community types--the EMERGENT and TRANSITION communities (Figure 28). It appeared in very low densities in the other communities by 1976 and 1977. *S. Eurycarpum* exhibited a small net increase in shoot density in the TRANSITION community, but decreased in shoot density in the EMERGENT type.

S. alba is a shrub species that generally occurs on topographically higher- and better-drained sites than the *CAREX STRICTA* community. Usually, a clump of *Spiraea* stems will shade the ground surface, reducing the types and densities of understory species. Because the presence of *Spiraea* identified a site as belonging to the *SPIRAEA* community, almost all the individuals of *Spiraea* counted were confined to the *SPIRAEA* community.

In both the area of major impact and the marsh as a whole, shoot density of *S. alba* increased for 2 yr after impact, peaking in 1976, and then decreased in 1977. In the area of major impact, shoot density was 2.3 stems/quadrat in 1974, rose to 7.4 in 1976, and decreased to 1.6 in 1977. For the whole marsh, shoot densities changed from 1.2 to 5.9 to 2.7 stems/quadrat for the same years. In both cases, the decrease in 1977 probably opened up substantial colonization space on the comparatively less-saturated substrate for numerous opportunistic species, like *P. pumila* and *E. coloratum*.

L. minor is a floating aquatic plant in which the tiny individual plants are blown across the surface of the water by the wind. Many hundreds of individual plants may accumulate in a square meter of water surface, especially where the wind has blown them in among the stalks of the emergent species. Because of its floating habit and nearly ubiquitous presence on still, open water, the presence of moderate to large numbers of *Lemna* can be used as an indication of the amount of open water in a community.

Figure 29 shows the estimated shoot density of *L. minor* over the whole marsh. A consistent general trend toward higher densities of *Lemna* in 1977 compared to 1974 was observed for all community types. This is the expected

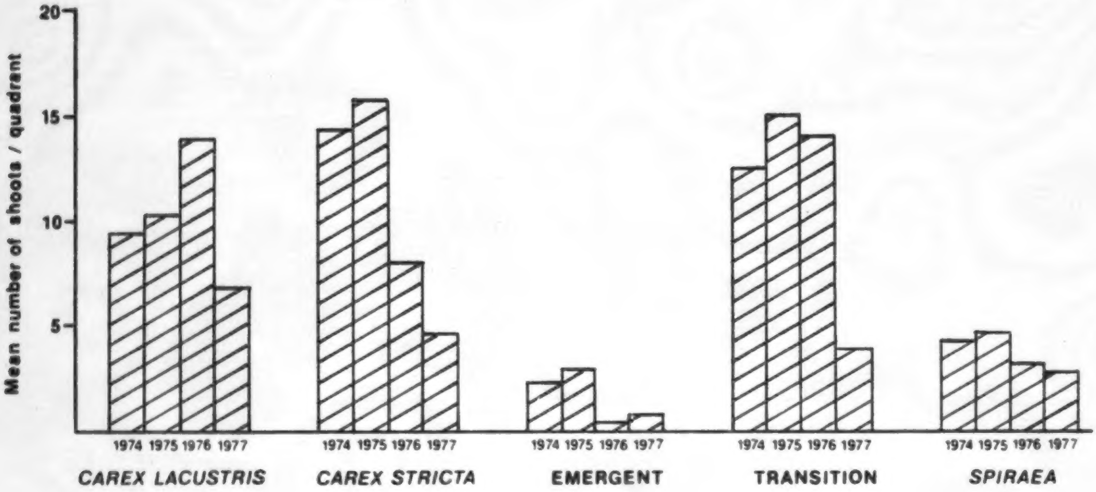

Figure 27. *Calamagrostis canadensis*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities for the entire sampling area.

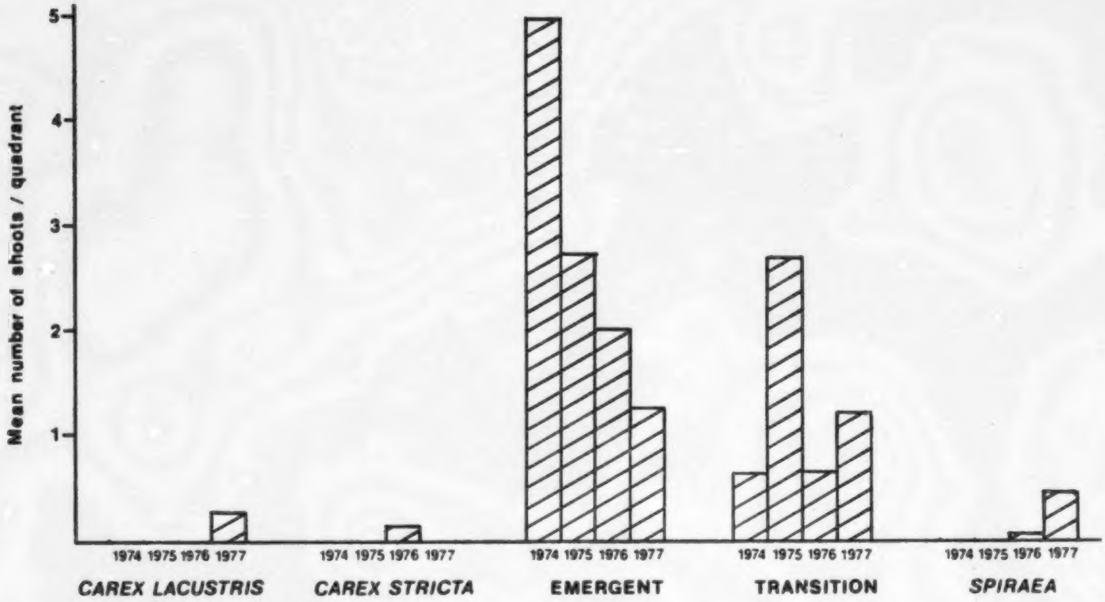

Figure 28. *Sparganium eurycarpum*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities for the entire sampling area.

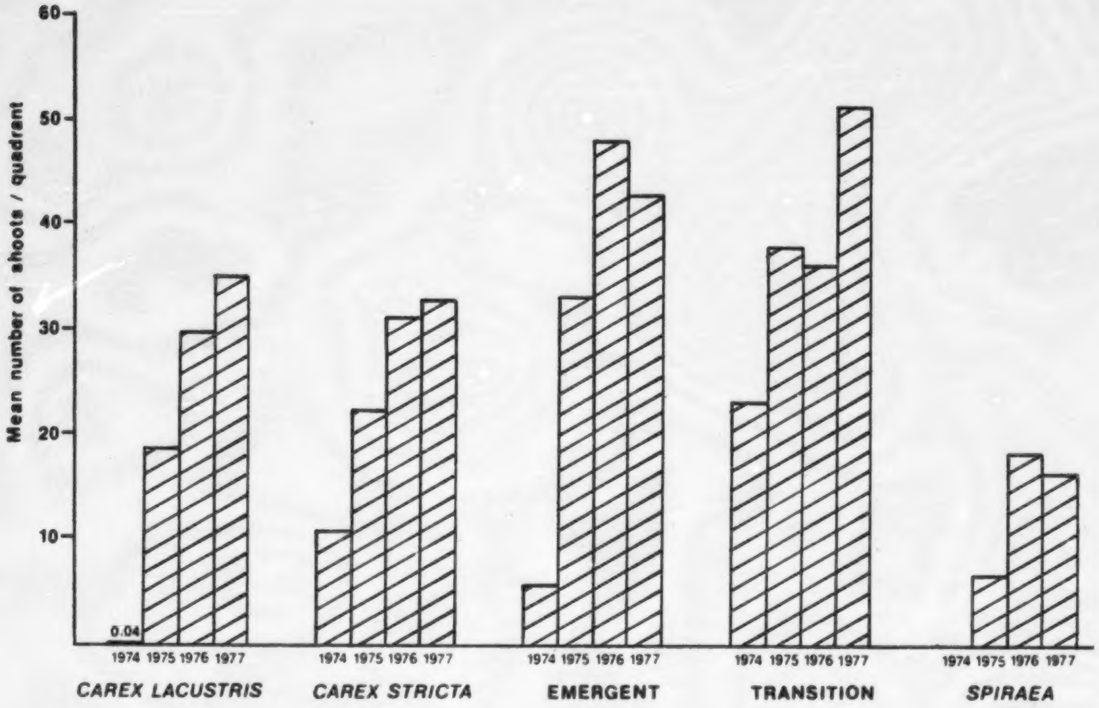

Figure 29. *Lemna minor*. Changes from fall 1974 to fall 1977 in mean number of shoots per quadrat (0.25 m^2) within five wetland plant communities for the entire sampling area.

result of an increased area of open water in the meadow/marsh community due to the combination of increased water depth and high mortality of dominant rooted species.

Species response in the area of major impact cannot be compared with that in the entire marsh for species reaching maximum density in summer. In 1976 and 1977, summer data were collected only for transects 18 to 30. Thus, a full comparison of summer data for the two areas through 1976 and 1977 is not possible for *S. latifolia, B. cernua,* or *P. pumila.* Fall data cannot be used for *Sagittaria* because it dies back comparatively early and decomposes rapidly (Lindsley et al. 1976). Although the decomposition is less complete, the same is true for *P. pumila* and *B. cernua.* Field observations indicate that densities of *Bidens* and *Pilea* increased in the entire marsh from 1974 to 1977, but to a lesser extent than in the area of major impact.

Community Responses to Perturbation--

Four measures were used to assess the response of wetland plant communities on the Columbia site to water level and heat stress:

1. $\overline{S}$ is mean number of species per quadrat.

2. S is total number of species for all quadrats sampled. S and $\overline{S}$ are measures of species richness.

3. $$H' = -\sum_{i=1}^{n} p_i \ln p_i \qquad (1)$$

where

H' is the Shannon-Wiener diversity index (Peet 1975) combining species richness and the distribution of abundances of individuals in the different species, and

p_i is the proportion of total number of individuals contributed by species i.

4. $$J = \frac{H'}{H'_{max}} = \frac{H'}{\ln S} \qquad (2)$$

where

J is the distribution of abundances in terms of their evenness or equitability and is the opposite of dominance; if J is low, dominance is high, and H'_{max} is the maximum value of H' for the given number of species (S) (Pielou 1975)

$\overline{S}$ was computed using the entire set of count data for the 50 x 50 m grid which varies in number of samples from year to year. However, S, H', and J, which vary with sample number (Peet 1975), were computed on uniform subsets of the data in order to allow comparisons to be made from year to year. Five subsets of equal sample number were selected randomly from the entire set of count data for each community for each sampling period. S, H', and J were computed for each random set. The individual values were used to calculate mean values--S*, H*, and J*--defined as the arithmetic mean of S, H', and J for the five random sets. Sample numbers for the full data set and the five random sets for each community and sampling period are shown in Table 3. Each measure was computed for each community for all sampling periods for the area of major impact and the entire sampling area.

A fifth measure, the proportion of quadrats containing no rooted vegetation, was calculated for the area of major impact. It is based on all data and considers all communities together. The proportion is the ratio of quadrats containing no rooted vegetation to the total number of quadrats sampled. A similar measure using the proportion of quadrats containing only annual vegetation also was calculated.

Results of community-level measures of wetland response to leakage from the Columbia cooling lake show significant changes occurring in the structure of the plant communities. Diversity (H*) and equitability (J*) decreased overall from 1974 to 1977. Species richness usually decreased initially but showed a net gain from summer 1974 to summer 1977 for most communities. Major decreases occurred in all values by summer 1975 and were similar throughout the sampling area. Subsequent responses varied for the two different sampling areas, from community to community, and for summer and fall sampling periods. The greatest magnitudes of change tended to be--but were not always confined to--the designated area of major impact.

Changes following perturbation in species richness (S and S*), equitability (J*), and diversity (H*) are discussed by community type. The *CAREX LACUSTRIS*, *CAREX STRICTA*, EMERGENT, and TRANSITION communities are compared for each of four data sets:

1. Transects 18 to 30 (summer set) cover the designated area of major impact for the summers of 1974 to 1977.

2. Transects 18 to 30 (fall set) cover the area of major impact for falls of 1974 to 1977.

3. Transects 1 to 40 (summer set) include data for the entire sampling area for 1974 and 1975.

4. Transects 1 to 40 (fall set) include data for the entire sampling area for falls of 1974 through 1977.

Within the area of major impact, sample size for the *CAREX STRICTA* and EMERGENT communities was small (8 and 10, respectively); results are interpreted accordingly and in light of additional information provided by results from the larger data set (transects 1 to 40). The SPIRAEA and LOWLAND SHRUBS and TREES communities are discussed separately because of small sample size in most data sets. Sample size is consistently large enough for trend analysis from 1974 through 1977 only for the fall data set for transects 1 to 40. Additional information on the *SPIRAEA* community is provided by a small data set (n = 10) for transects 1 to 40 for summers 1974 and 1975. Results from the four data sets are summarized in Figures 31 to 34 and Tables A-1 to A-4 of Appendix A.

TABLE 3. SAMPLE NUMBERS FOR THE FULL DATA SET AND UNIFORM RANDOM SUBSETS FOR EACH COMMUNITY[a] AND SAMPLING PERIOD

Sampling period	Communities for transects 18 to 30						Communities for transects 1 to 40					
	A	B	C	D	E	F	A	B	C	D	E	F
FULL DATA SET												
Summer 1974	16	8	16	10	2	2	40	46	40	26	10	6
Summer 1975	17	8	14	18	6	2	55	56	38	44	16	14
Summer 1976	28	18	26	20	8	10						
Summer 1977	28	18	24	22	8	10						
Fall 1974	10	10	10	10	6	4	26	38	32	26	16	27
Fall 1975	22	12	12	10	8	7	48	91	38	30	20	64
Fall 1976	22	15	16	18	8	8	42	55	40	32	19	39
Fall 1977	28	17	24	19	8	9	76	99	69	51	26	63
UNIFORM RANDOM SUBSETS												
Summer 1974-77	16	8	14	10	2	2	40	46	38	26	10	6
Fall 1974-77	10	10	10	10	6	4	26	38	32	26	16	27

[a] A is *Carex lacustris*, B is *Carex stricta*, C is Emergent, D is Transition, E is *Spiraea*, and F is Lowland Trees and Shrubs.

CAREX LACUSTRIS community--The pattern of response for the *CAREX LACUSTRIS* community in the designated area of major impact was one of major decreases in all values followed by significant increases in all values after a period of little to moderate change (Figure 30). Prior to disturbance, the *CAREX LACUSTRIS* community had higher values for species richness ($\bar{S} = 5.88$), species number ($S^* = 26$), and diversity ($H^* = 2.36$) than any other community in the area of major impact. It also had the highest values for species number ($S^* = 31$), species richness ($\bar{S} = 7.46$), and diversity ($H^* = 2.18$), as well as for equitability ($J^* = 0.63$) in 1977, i.e., two full years after the generating station began operation. In the case of $\bar{S}$ and S^*, 1977 values were higher than 1974 values.

Between summer 1974 and summer 1977 the *CAREX LACUSTRIS* community experienced marked decrease and marked increase in community measures. From 1974 to 1975, the community lost a greater number of species ($\Delta\bar{S} = -1.8$, $S^* = -7.6$) than any other community. At the same time, diversity (H^*) dropped dramatically ($\Delta H^* = 0.68$) and a shift toward greater dominance occurred, as evidenced by a drop in J^* of 0.14. Equitability continued to drop through summer 1976. Diversity, however, increased slightly ($\Delta H^* = +0.01$), apparently as a result of the moderate increase in species richness ($\Delta\bar{S} = 0.88$) and species number ($\Delta S^* = 4.4$). From summer 1976 to summer 1977 species richness and species number in the *CAREX LACUSTRIS* community showed the greatest change seen in these measures in any community for any sampling year, increases of 2.5 and 8.0 for $\bar{S}$ and S^*, respectively. With 1977 values for $\bar{S}$ and S^* exceeding 1974 values, diversity ($H^* = 0.63$) returned to within 0.09 of its pre-treatment value. Equitability, likewise, returned to near its 1974 value.

Fall data for the designated area of major impact show essentially the same trends for community-level measures as the summer data (Figure 31). A notable exception for the fall data is a reversal in the direction of change shown from summer 1975 to summer 1976. Fall values for species richness ($\bar{S}$), species number (S^*), and diversity (H^*) fell from 1975 to 1976; equitability (J^*), on the other hand, increased. Fall 1976 to 1977 changes in richness and diversity were in the same direction as summer 1976 to 1977 trends but the increases were less dramatic. Equitability (J^*) remained at its 1976 value, 0.09 below its pre-treatment value.

Data analyzed for the area of major impact (Figures 30 and 31) show somewhat different patterns of response than the data sets (3 and 4 earlier) for the *Carex lacustris* community taken over the entire sampling area (transects 1 to 40) (Figures 32 and 33). Differences appear in direction and magnitude of change, the overall pattern suggesting that before summer 1976 the area north of transect 30 was responding to different types or magnitudes of disturbance than the area south of transect 30.

Summer values of S^*, H^*, and J^* for the entire marsh dropped from 1974 to 1975, as they did in the area of major impact. However, the magnitude of the decreases were less. Given the contribution from the area of major impact to these measures for the entire area, they likely decreased very little. Equitability had dropped considerably within the area of major impact from 1974 to 1975, but changed little for the entire sampling area.

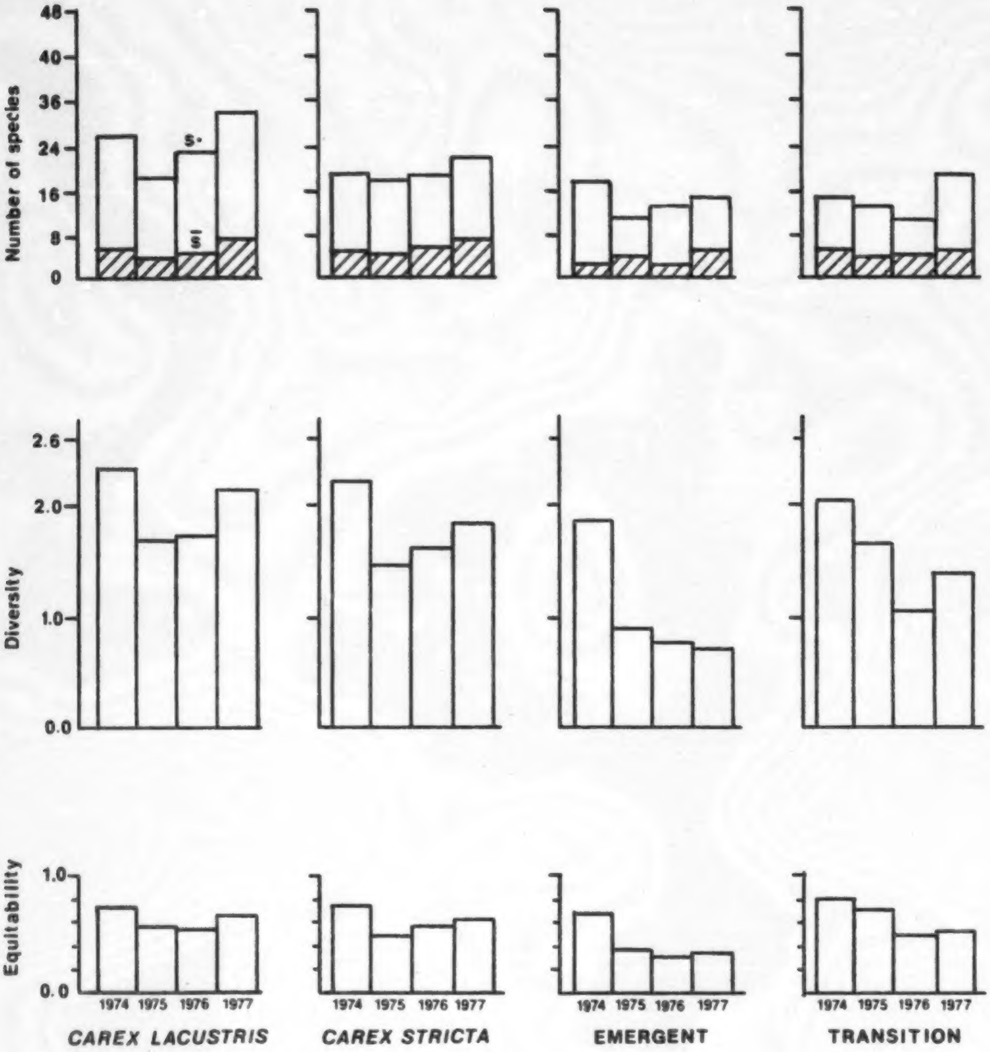

Figure 30. Community measures before (1974) and following disturbance (1975 to 1977) for four wetland plant communities. Data presented are summer data for the area of major impact. (S and $\overline{S}$ are measures of species richness; H' is the Shannon-Weiner diversity index; J is distribution of abundances in terms of equitability.)

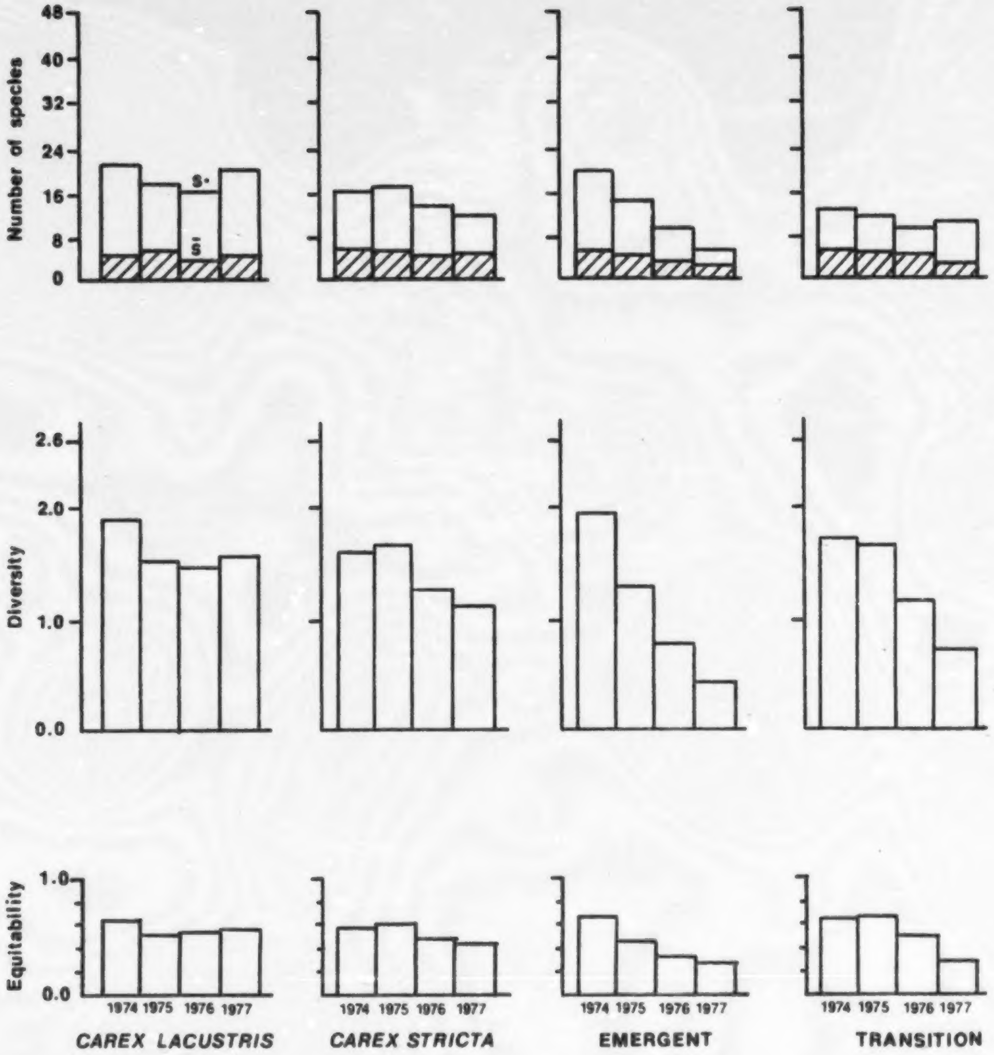

Figure 31. Community measures before (1974) and following disturbance (1975 to 1977) for four wetland plant communities. Data presented are fall data for the area of major impact. (S and $\bar{S}$ are measures of species richness; H' is the Shannon-Weiner diversity index; J is distribution of abundance in terms of equitability.)

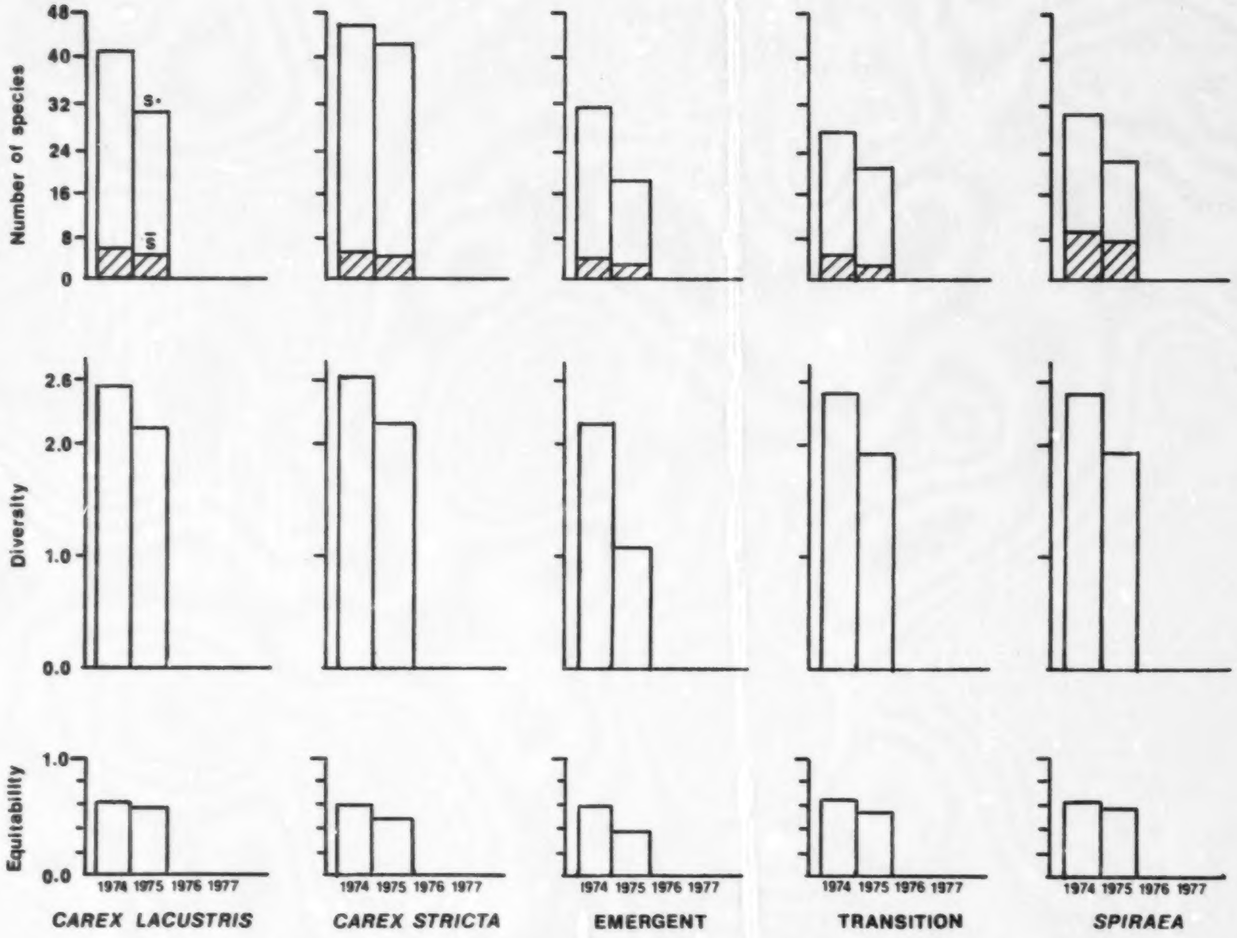

Figure 32. Community measures before (1974) and following disturbance (1975 to 1977) for six wetland plant communities. Data presented are summer data for the entire sampling area. (S and $\overline{S}$ are measures of species richness; H' is the Shannon-Weiner diversity index; J is distribution of abundances in terms of equitability.)

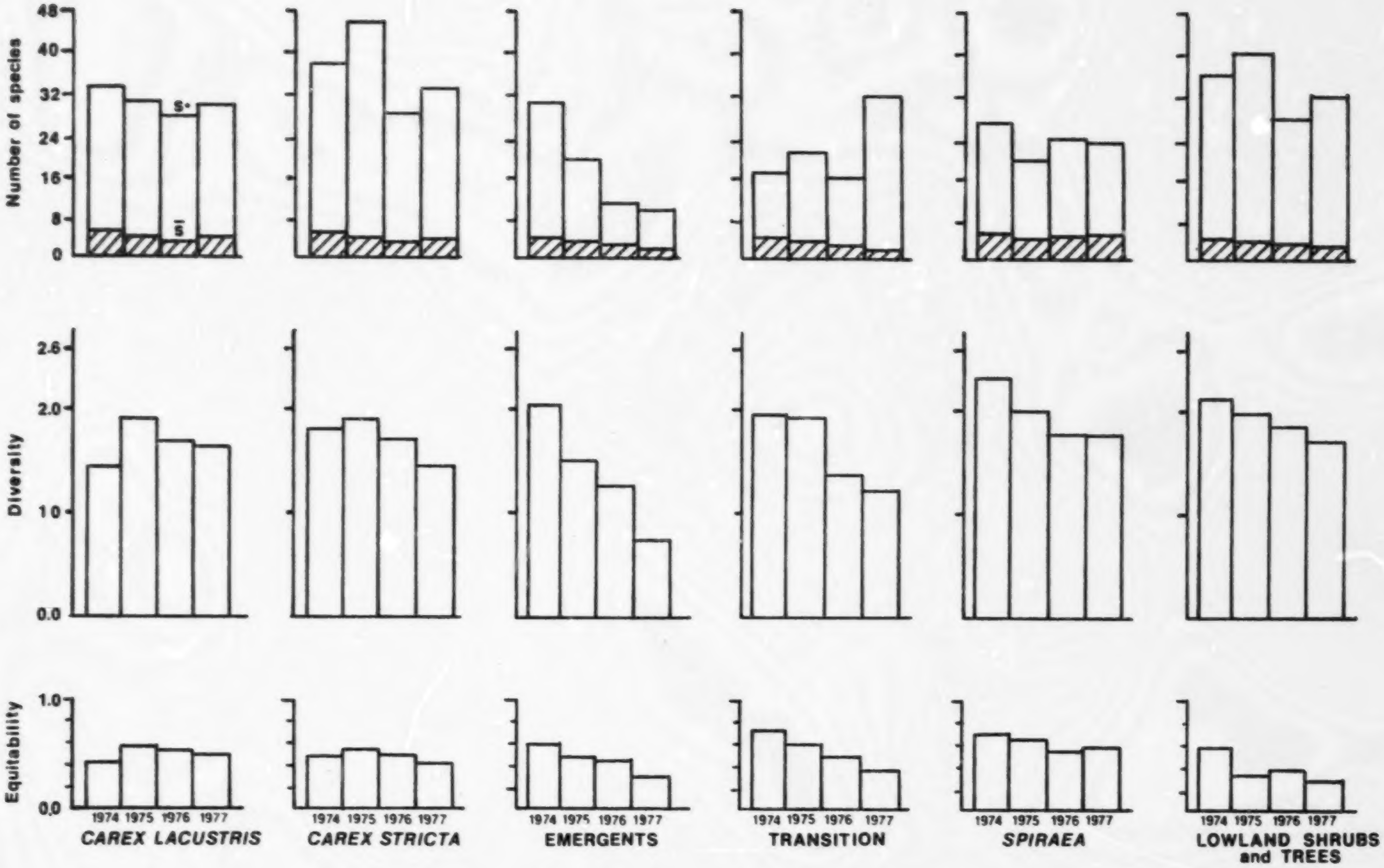

Figure 33. Community measures before (1974) and following disturbance (1975 to 1977) for six wetland plant communities. Data presented are fall data for the entire sampling area. (S and $\overline{S}$ are measures of species richness; H' is the Shannon-Weiner diversity index; J is distribution of abundances in terms of equitability.)

This suggests that south of transect 30 equitability actually increased somewhat from 1974 to 1975.

In the case of fall data for 1974 to 1975, the direction of change in $\overline{S}$, H*, and J* is reversed from that for transects 18 to 30. The magnitude of increase in these measures over the entire sampling area was as great as the magnitude of the decrease in the area of major impact. However, for S* the direction and magnitude of change were similar.

After 1975, data collected outside the area of major impact exist only for fall. It shows that differences in the patterns of response for the two sampling areas were not as great after 1975 as they were from 1974 to 1975. The overall pattern suggests that community level effects spread from 1975 to 1977 over a greater and greater portion of the area south of transect 30. From 1975 to 1976 only the direction of change in J* and the magnitude of the decrease in H* differ between the two sampling areas. All values dropped moderately--except for J* for the area of major impact and H* for the entire sampling area--which increased. Diversity dropped almost twice as much as H* for the area of major impact. Apparently, although decreases in species number (S*) occurred immediately, significant shifts toward greater dominance were delayed for 1 yr in the *CAREX LACUSTRIS* community south of transect 30.

Diversity in the entire sampling area continued to drop from fall 1976 to fall 1977, while in the area of major impact diversity reversed direction and began to increase. Furthermore, J* continued to decline for the entire sampling area, whereas in the area of major impact it remained constant. At the same time S* rose sharply in the area of major impact. The small gain in S* over the entire area, considered against the large increase in the area of major impact, indicates an actual decrease in species number from 1976 to 1977 south of transect 30. Considered together, the three data sets suggest that major community-level effects were somewhat delayed south of transect 30.

CAREX STRICTA community--The *CAREX STRICTA* community showed a pattern of marked decreases and increases. Trends shown in the summer data for both sampling areas (Figure 30, Figure 32) were remarkably similar to those for the *CAREX LACUSTRIS* community. The only notable exceptions were the smaller decrease in species number (S*) from 1974 to 1975 and the greater increase in diversity from 1975 to 1976. In general, community measures for the *CAREX STRICTA* community decreased significantly from summer 1974 to summer 1975. In the area of major impact, values generally increased after 1975. By 1977, species richness and species number ($\overline{S}$ and S*) exceeded 1974 values; diversity (H*) and evenness (J*) increased after 1975 but failed to return as close to their 1974 values as they had in the *CAREX LACUSTRIS* community.

As in the *CAREX LACUSTRIS* community, summer 1974 to 1975 response patterns for the entire sampling area and the area of major impact showed decreases in species richness ($\overline{S}$)and species number (S*). Likewise, the concomitant decreases in diversity (H*) and equitability (J*) were greater in the area of major impact than for the meadow/marsh as a whole.

Trends in the fall data (Figure 31, Figure 33) from 1974 to 1977 in the area of major impact, were largely the opposite of those for the *CAREX LACUSTRIS* community. In general, values increased from 1974 to 1975 and dropped from 1975 to 1977 to well below their 1974 values. With the exception of species number (S*), which fluctuated widely over the entire sampling area, trends for the entire sampling area were similar but of lower magnitude than fall changes in the area of major impact.

EMERGENT community--The greatest net change occurred in the EMERGENT community. Changes were immediate, generally of greater magnitude than changes elsewhere, and nearly uniform in direction (Figures 30 to 33). Values for all community measures decreased consistently from 1974 to 1977. The only exceptions were species richness ($\overline{S}$) which increased from 1976 to 1977, and species number (S*), which climbed after 1975 in the area of major impact. Otherwise, patterns of response were remarkably similar for the entire sampling area and the area of major impact.

Prior to disturbance, the EMERGENT community had lower summer values in both sampling areas for $\overline{S}$, H*, and J* than any other community. From 1974 to 1977, the EMERGENT community showed the greatest net change in diversity ($\Delta H^* = -1.10$) and equitability ($\Delta J^* = -0.35$) seen in any community. By 1977, summer values for all measures were lower than in any other community in the area of major impact the greatest decrease occurred from 1974 to 1975.

Fall patterns were similar but the decreases were more uniformly distributed from year to year. The values of S*, H*, and J* decreased to a greater extent in the area of major impact than in the entire marsh.

TRANSITION community--Like the EMERGENT community, changes in the TRANSITION community follow similar overall patterns for the entire marsh and the area of major impact (Figure 30, Figure 33). Prior to disturbance, the TRANSITION community, considered over the entire sampling area, had the lowest value for species number ($S^* = 26$), but the highest value for equitability ($J^* = 0.78$). Following disturbance, summer values decreased from 1974 through 1976 for all measures. From 1976 to 1977, species number (S*) rose to above its 1974 value; diversity (H*) and equitability (J*) began to increase but remained well below 1974 values.

Fall data do not show the 1976 to 1977 change in direction of response. Most values continued to decline through 1977. The exception was species number (S*), which increased dramatically in the entire sampling area. Species richness ($\overline{S}$), which usually paralleled species number (S*), followed H* and J* in continued decline through fall 1977.

Although the overall pattern is similar for both sampling areas, notable differences occurred in the magnitude of the response. Initial decreases seen in the summer data from 1974 to 1975 were--except for species number (S*)--somewhat greater for the entire marsh than for the area of major impact. However, differences seen in the fall data show greater change in the area of major impact. Greater net decreases in all values except S* occurred from fall 1974 to fall 1977 in the area of major impact.

Decreases from fall 1976 to fall 1977 in species richness ($\bar{S}$), diversity (H*), and equitability (J*) also were greater in the designated area of major impact.

SPIRAEA and LOWLAND SHRUBS and TREES communities—The restricted data available for the *SPIRAEA* and LOWLAND SHRUBS and TREES communities (Figure 32, Figure 33) show net decreases from fall 1974 to fall 1977 in all measures for both communities. As in other communities, significant changes occurred by 1975. Species number (S*) increased in the LOWLAND SHRUBS and TREES community from 1974 to 1975. All other values decreased in both communities.

After 1975, fall values for diversity (H*) declined continuously in both communities. Species richness ($\bar{S}$) decreased each year for the LOWLAND SHRUBS and TREES community. Other fall values increased and decreased. Only species richness in the *SPIRAEA* community returned by 1977 to near its 1974 value.

Changes in Vegetative Cover--

In addition to major shifts in dominance and diversity patterns in each plant community, a continuing trend of decreasing vegetative cover occurred in the Columbia wetlands from 1974 to 1977. Open water and exposed mudflats replaced the previously closed and densely vegetated perennial plant communities over an increasing portion of the study area (Figure 34). Annuals colonized some of the habitat opened by the removal of perennial species, but large areas remained unvegetated. By 1977, 19% of the quadrats sampled in the area of major impact had no rooted vegetation. Another 2% contained only annual vegetation (Figure 35).

DISCUSSION AND CONCLUSIONS

Changes in plant population numbers, vegetative cover, species richness, diversity, and equitability such as those seen in all wetland communities on the Columbia site reflect major changes in the composition and structure of the plant communities. The trends toward a greater abundance of hydrophytic species and decreasing vegetative cover follow the expected pattern for wetlands subject to increased and/or more constant water levels (Weller and Fredrickson 1974, Van der Valk and Davis 1978b). The predominant trend of decreasing diversity from 1974 to 1977 also follows an expected trend. However, the year-to-year and specific community patterns of response shown in the diversity data did not follow a single trend and were not readily interpretable. As data for the different communities reveal, no uniform monotonic relationship existed between disturbance and species diversity--neither species richness nor distribution of their abundances. Disturbance did not simply increase or decrease plant diversity. Species richness ($\bar{S}$ and S*), diversity (H*), and equitability (J*) all decreased in most cases, but increased in others, and frequently did both during the period from 1974 to 1977 in the Columbia wetlands as the spatial distribution and intensity of the disturbance increased.

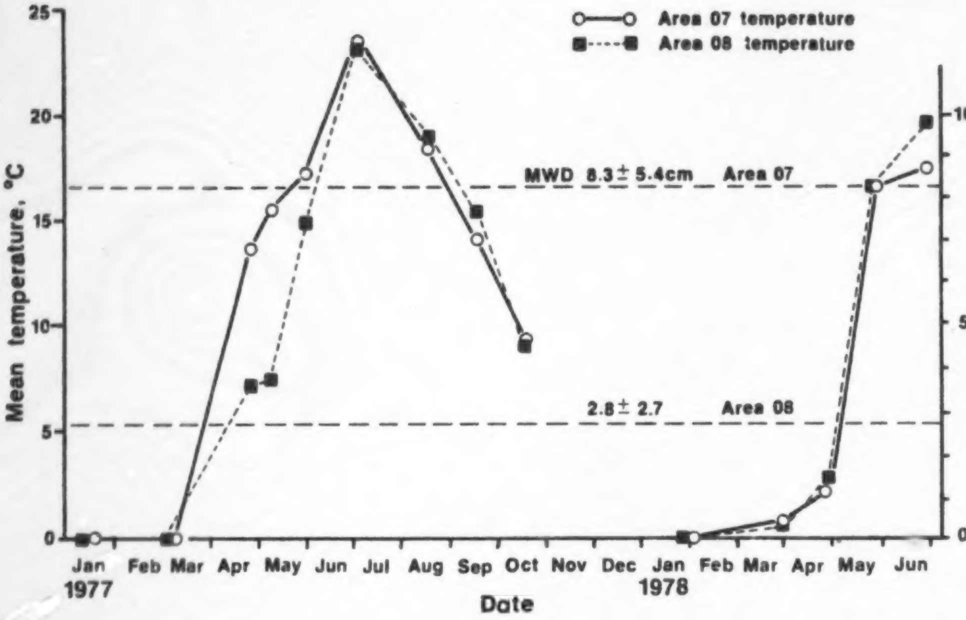

Figure 34. Temperature patterns in the substrate and mean water levels (± s.d.) at control sites for *Typha latifolia* (Area 07) and *Carex lacustris* (Area 08).

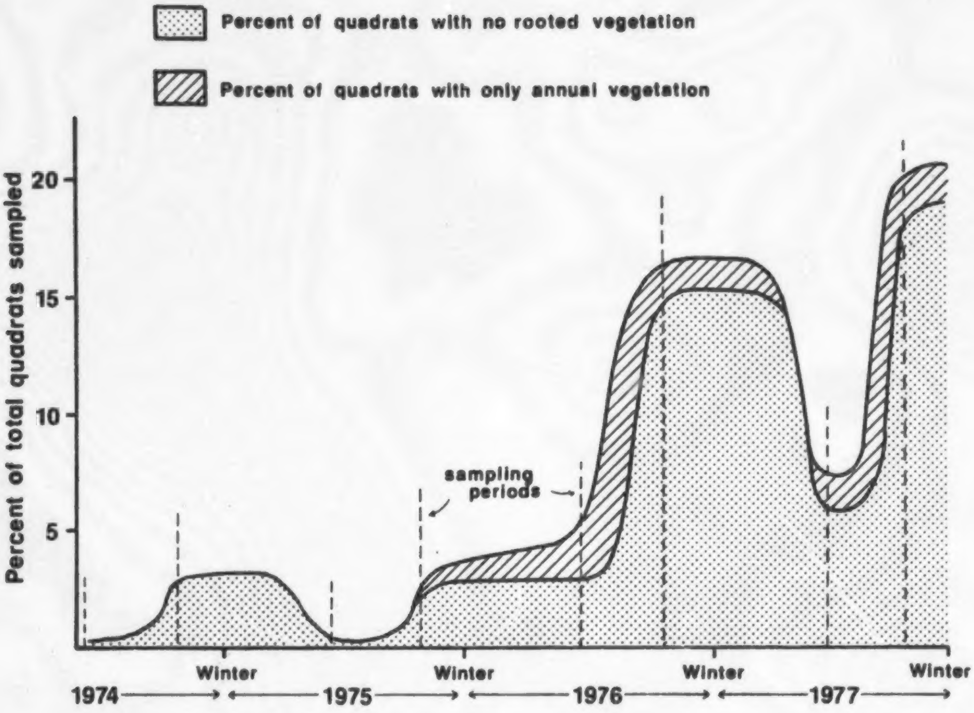

Figure 35. Changes in vegetative cover from 1974 to 1977.

The data for individual plant populations considered together with the results for measures of community response suggest that differences in diversity patterns observed between communities, and between the area of major impact and the entire sampling area, can be explained by two factors: 1. The spatial and temporal patterns of disturbance, and 2. the comparative sensitivity of dominant plant species to disturbance (Harper 1969, Lubchenco 1978, Caswell 1978). Where disturbance was of the type to which dominant species were sensitive, diversity and equitability increased as new or competitively inferior species colonized or spread to space made available by the decline of previously dominant populations. Diversity and equitability decreased where one or two dominant species were favored by the disturbance.

Changing diversity patterns paralleled changing temporal and spatial patterns of disturbance. From 1974 to 1975, the entire area was subject to the same disturbance, i.e., permanently elevated water levels and increased groundwater discharge. All communities in both sampling areas responded similarly. Species richness, diversity, and equitability dropped in all communities. This appears to be the result of density decreases in some dominants, the removal of some non-dominant species by flooding, and the concomitant and dramatic increase of *L. minor* in newly-available open water areas. The greater magnitude of the decrease in the area of major impact for the *CAREX LACUSTRIS* and *CAREX STRICTA* communities may reflect the generally higher discharge rates and lower topographic position of these communities north of transect 30.

After spring 1975, disturbance patterns became more complex as an increasing area of the marsh experienced temperature changes. Significant changes in temperature were localized at first, spread only gradually, and have not yet reached equilibrium. In general, the *CAREX LACUSTRIS* and *CAREX STRICTA* communities were subject to more heat stress earlier because they tended to be located nearer the dike than the major portions of the TRANSITION and EMERGENT communities. Both the TRANSITION and EMERGENT communities, however, were subject to low-level temperature changes resulting from high groundwater discharge and surface water flow. Surface water froze later in winter and thawed earlier in spring. Major flow channels remained open throughout the year.

After 1975, diversity patterns among communities became more complex. Each community responded differently. Species richness usually increased but diversity and equitability decreased in some communities and increased in others. It is believed that differences in diversity patterns can be accounted for by the differential behavior of a community's dominant species responding to different types and magnitudes of disturbance.

Plant population data show that dominant species were not equally sensitive to flooding, heat stress, or increased surface water flow. Some species such as *C. lacustris* and *C. rostrata*, were extremely sensitive, declining rapidly and dramatically in all communities. Other perennial species, such as *C. stricta* and *Calamagrostis canadensis*, responded more slowly, decreasing only after 1976. *T. latifolia*, on the other hand, increased continuously in the EMERGENT community and invaded all other communities.

The population data also show that dominant species differed among communities in their abundance and distribution. All of the abovementioned species were abundant prior to disturbance. All except *C. rostrata* and *T. latifolia* were widely distributed. However, *C. rostrata* was abundant in only the TRANSITION and EMERGENT communities. *T. latifolia* was restricted for the most part to the EMERGENT community. In the *CAREX LACUSTRIS* community, *C. lacustris* was co-dominant with *C. stricta*. *C. stricta* clearly dominated the *CAREX STRICTA* community. The TRANSITION community had no single dominant. *C. canadensis* and *C. stricta* were nearly equal in relative abundance with *C. rostrata* and *C. lacustris* only slightly less abundant. The EMERGENT community--though locally dominated by *T. latifolia*--contained large relative abundances of *C. rostrata* and *C. lacustris*.

Communities dominated by sensitive species exhibited different temporal trends than did those communities in which dominant species were tolerant of the stress or favored by it. In the *CAREX LACUSTRIS* and *CAREX STRICTA* communities, species richness, diversity, and equitability increased after 1975, more so in the *CAREX LACUSTRIS* community than the *CAREX STRICTA* community. The increases coincided with the decline of *C. lacustris*, which was eliminated from both communities by 1977. The slight differences in the magnitude of the response appear to be related to the greater sensitivity of *C. lacustris* and its greater abundance in the *CAREX LACUSTRIS* community compared with the greater tolerance of *C. stricta* and its dominance in the *CAREX STRICTA* community. More habitat was made available for new or expanding species by the proportionately greater decrease in populations of *C. lacustris* in the *CAREX LACUSTRIS* community. Species richness, diversity, and equitability in that community all increased to near or above 1974 values.

In contrast, diversity declined further and equitability remained low in the EMERGENT community after 1975, despite increases in species number. Two tolerant species, *L. minor* and *T. latifolia*, increased continuously through 1977, while other species declined in abundance. Diversity and equitability decreased as disturbance increased the relative dominance of *Lemna* and *Typha*.

The pattern of response in the TRANSITION community followed the fate of sensitive and tolerant dominant species. Species number, diversity, and equitability declined less rapidly from 1974 to 1975 than other communities due to the balancing of increases and decreases among the dominants depending on their sensitivity to flooding and high surface water flow. Major decreases in diversity and equitability occurred from 1975 to 1976 as *L. minor* became exceedingly dominant. Diversity increased after 1976 following the decline of *C. lacustris* and *C. rostrata*. The addition of a number of species to the community--as colonization space became available with the decline in dominant species--accounted for the increase.

The ecological significance of community patterns of response is not evident from the diversity data alone. No uniform relationship was observed between diversity and intensity of disturbance. The different diversity measures sometimes varied independently and showed decreases and increases with disturbance. Decreasing values in the EMERGENT community did not correspond to a greater degree of disturbance than in the SEDGE MEADOW communities. Increasing diversity values in the SEDGE MEADOW communities after 1975 did not indicate a recovery process or return to pre-impact composition or structure. Examination of the population and community data showed that return of diversity values to near or above pre-impact values paralleled the continuing decline of dominant perennial sedges and their replacement by annuals or short-lived perennials as the magnitude and spatial scale of disturbance increased.

Considered together, the Columbia population and community data sets show that increases in diversity under non-equilibrium conditions may represent continuing disturbance rather than recovery of the system or "advance" in successional stage brought about by establishment or competitive interactions of long-lived perennials. Diversity measures must be interpreted in light of population data and the behavior of dominant species. Diversity theory is not sufficiently well-developed for non-equilibrium communities for vegetation changes to be evaluated on the basis of diversity measures alone (Caswell 1978, Green 1979).

SECTION 4

SEASONAL CHANGES IN PHENOLOGY AND CARBOHYDRATE RESERVES OF *TYPHA LATIFOLIA* AND *CAREX LACUSTRIS* POPULATIONS SUBJECT TO ALTERED TEMPERATURE AND FLOODING PATTERNS

INTRODUCTION

The wetland plant study of the Columbia Project was undertaken to monitor vegetation changes associated with leakage from the cooling lake of the Columbia Electric Generating Station. Results of the monitoring program showed significant vegetation changes within 1 yr of Columbia station operation (section 3, Bedford 1977). However, freshwater wetlands in the upper Midwest may undergo natural shifts in species composition and structure without being subject to human-induced environmental influences (Bedford et al. 1974, Van der Valk and Davis 1978b, Weller and Fredrickson 1974).

The research goals for this study had to go beyond documenting the resultant changes in communities to understanding how exogenous disturbances affected the actual process of change. Such studies are essential if field techniques are to be developed for determining in advance of facilities' development the probable effects of waste heat and elevated groundwater levels on wetland plant communities. The principal research objectives included determination of:

1. Causal mechanisms potentially relating vegetation changes to environmental variables that could be associated with leakage from the cooling lake.

2. The magnitude of effect resulting from known levels and combinations of environmental factors produced by leakage from the cooling lake.

3. Ecologically based criteria by which significant impact to wetland plant communities could be recognized, monitored, and predicted in the field at the species level, given particular factor levels for the environmental variables.

Meeting these objectives required characterizing the sequential field behavior of individual species responding to stress, i.e., identifying the various stages and associated mechanisms in the course of population response for individual species.

This paper reports the seasonal response of *Typha latifolia* and *Carex lacustris* populations to mild heat and water stress as measured by monthly data on shoot number, height, and chlorosis. It examines alterations in plant phenology and corresponding changes in amounts of carbohydrate stored in or depleted from rhizomes, shoots, and shoot bases as the causes of population decline.

The mechanisms controlling population dynamics of perennial rhizomatous species were hypothesized to be heat-induced variations in plant phenology and plant metabolism. It was thought that vegetation changes related to waste heat would be exhibited by variations in temperature-regulated phenomena: 1. Metabolic processes, such as photosynthesis, respiration, and translocation of photosynthate; and 2. plant phenology, such as timing of shoot emergence, growth, and dieback.

Specifically, it was hypothesized that winter groundwater temperatures in excess of those normally prevailing during periods of winter dormancy for Wisconsin wetland plants would result in: 1. Exhaustion of energy reserves stored in underground organs and over-wintering shoots of dominant perennial plants; 2. altered timing of shoot emergence, growth, and dieback; and 3. subsequent population decline.

Perennial wetland plants of northern latitudes generally follow a cycle of accumulation of photosynthetic products during the growing season, high levels of storage (with some depletions) during winter dormancy, followed by rapid translocation and depletion of stored energy reserves during spring growth. Temperatures out of phase with normal cycles of plant growth alter temporal patterns of plant growth and the storage or depletion of reserve materials. Wetland species such as cattail (*Typha* spp.) allocate a large percentage of their biomass production to over-winter reserves of non-structural carbohydrates stored in rhizomes (Gustafson 1976). The importance of these reserves for early spring growth has been shown for *Typha* by McNaughton (1974), Linde et al. (1976), and Gustafson (1976) and postulated for *Carex rostrata* by Bernard (1974). Bernard and Bernard (1973) further stressed the considerable significance of winter biomass in wetland ecosystems. Heat-induced high rates of winter respiration or winter shoot emergence depletes the energy supply required for spring shoot emergence and growth, thus reducing shoot number and causing population decline.

METHODS

Selection of Species

Two species (*T. latifolia* and *C. lacustris*) were selected for study on the basis of field observations of species response, data from semi-annual vegetation sampling (section 3, Bedford 1977), a review of literature pertaining to the autecology of species dominant in the Columbia wetlands, and field studies of measurement techniques to determine feasibility for use with a particular species.

On 1 April 1976, qualitative field observations were initiated to characterize seasonal behavioral responses of individual plant species in localized areas subject to temperature changes. During twice-weekly field inspections phenological data (e.g., onset of shoot emergence, flowering, fruiting, and dieback) and obvious changes in plant vigor (e.g., chlorosis or loss of turgor) were noted. Observations were used to determine key field characteristics of species response to altered temperature and indentify sensitive species exhibiting clear and obvious field signs of stress.

Data from the 1974 and 1975 semi-annual vegetation sampling were used to determine which species were of sufficient importance in the Columbia wetland communities to affect significantly the course of community response. Criteria for selection included dominance in a single community or abundance in more than a single community.

A review of the literature was undertaken to: 1. Ascertain the importance of particular species in wetland systems, and 2. obtain information on the autecology and potential physiological response of specific wetland plants to changes in water temperature, water levels, and surface flow patterns. Existing information on life history and phenology of undisturbed populations was of particular interest. This could be used as a guide in experimental design and as a standard against which to evaluate species response on the Columbia site (Bedford et al. 1976 for *Carex* spp., Bedford 1979 for *Typha*).

Having made a preliminary selection on the basis of the above criteria, small-scale field studies were conducted to determine the feasibility of using those species for the proposed approach. The study site and nearby wetlands were reconnoitered to locate control and treatment stands of similar density and of adequate area to permit repeated sampling of species meeting this criteria. The rhizomes of six were excavated and washed to determine collecting and washing time, as well as the possibility of separating rhizomes from other plant parts and dead organic matter. Feasibility criteria included:

1. Existence of a control population located off-site with stand density similar to on-site population stands,

2. All stands of 25 m^2 minimum area,

3. Rhizomes, shoots, and shoot bases readily identifiable and separable from other plant parts,

4. Cumulative collecting time for all stands $<$ 7 days under winter conditions, $<$ 3 days for October conditions, and $<$ 2 days for May conditions,

5. Washing time for each sample $<$ 4 h.

Location of Sampling Sites

As is usually the case when working under field conditions, an ideal statistical design with simultaneous controls on all variables was not possible. Ideally, sampling sites should be selected to cover the possible range and combinations of environmental factors. However, the number and spatial distribution of adequate *Typha* and *Carex* stands constrained the number of available sites. No site was subject to temperature increases without the associated continuous saturation or flooding of the soil surface. Control sites were subject to neither change. Further, at the time of site selection, fine-scale information on the temporal and spatial distribution of disturbance factors was not available. Therefore, a combination of available broad-scale information and actual field responses of *Typha* and *Carex* as indicators of environmental conditions was used to select sites that represented what was believed to be the existing range of mean water levels and temperature increases on the Columbia site. Distance from the west dike of the cooling lake and winter ice conditions also were used as indicators of temperature patterns. In general, temperature increases attenuated with increasing distance from the dike. The location of sampling sites and characteristics known at the time of selection are summarized in Table 4 for five *Carex* sites and five *Typha* sites, including controls.

Plant Phenology

Shoot number, height, and chlorosis were selected on the basis of 1976 field observations as obvious field characteristics that could be easily measured at several sites on a repeated basis. Measures of each of these characteristics were recorded monthly in 15 random 0.2 m^2 circular quadrats at each of five sites for *Typha* and four for *C. lacustris* from February to October 1977 and from March to July 1978. A fifth site was added for *C. lacustris* in September 1977 and used only for phenological data. All live shoots were counted. Height was measured as distance from the soil surface to the tip of the longest leaf. Chlorosis was determined qualitatively in three broad categories: 1. Most shoots retaining color, < 40% chlorosis evident; 2. most shoots retaining some color, 40 to 80% chlorosis evident; 3. most shoots retaining little to no color, > 80% chlorosis evident.

Carbohydrate Reserves

All rhizomes, shoot bases, and new shoots within four 0.07 m^2 quadrats were collected at each of the same five *Typha* sites and four *Carex* sites in January, May, and October 1977, and January 1978. Time of sampling was determined using Bernard's life history data on *C. lacustris* (Bernard and MacDonald 1974, Bernard 1975, Bernard and Bernard 1977, Bernard and Solsky 1977) and the work of Gustafson (1976) and Linde et al. (1976) on *Typha* phenology and carbohydrate reserves. Sampling was scheduled to coincide with mid-winter carbohydrate storage (January), during spring shoot emergence and growth (late May), and just after the onset of dormancy, when reserves should be at a maximum value (late October). A chain saw was used to obtain frozen samples and a metal cover for non-frozen samples. Frozen samples were returned to the laboratory, thawed at room temperature, and washed to remove soil and extraneous plant debris. Non-frozen samples were washed immediately on site or transported in ice chests containing dry ice to the laboratory for washing. All identifiable rhizomes, shoots, and shoot bases or parts thereof were retained intact after washing. These were

TABLE 4. LOCATION AND CHARACTERISTICS OF SAMPLING SITES

Sampling area	Species[a]	Distance from west dike (m)	Mid-winter condition[b]	Temperature increase	Mean water level (cm)
01	*C. lacustris*	50	F	Moderate	$\leq$ 10
02	*C. lacustris*	50	0	Moderate	$\leq$ 10
03	*T. latifolia*	25	0	Maximum	$\leq$ 10
04	*T. latifolia*	350	F	Minimum	10 to 20
05	*T. latifolia*	325	0	Minimum	10 to 20
06	*T. latifolia*	150	0	Moderate	10 to 20
07[c]	*T. latifolia*	off-site	F	None	$\leq$ 10
08[c]	*C. lacustris*	off-site	F	None	$\leq$ 10
09	*C. lacustris*	25	0	Maximum	10 to 20
10	*C. lacustris*	50	F	Minimum	$\leq$ 10

[a] *C. lacustris* is *Carex lacustris*, *T. latifolia* is *Typha latifolia*.
[b] F is frozen, 0 is open water.
[c] Control sites.

wrapped in aluminum foil, submersed for several minutes in liquid nitrogen to stop metabolic activity, and stored at < 0°C.

Prior to laboratory analysis, samples were thawed at room temperature, dried for at least 48 h in a forced-air oven at 70°C, weighed, and ground in a Wiley mill. The modified Weinmann method of Smith (1969) was used to quantify total nonstructural carbohydrates.

Environmental Factors

Water depth, surface water temperature, and substrate temperature at each quadrat sampled were recorded for shoot counts and carbohydrate reserves. Water temperatures were taken 15 cm below the water surface or just above the soil surface if water depth was < 15 cm. Substrate temperatures were taken 15 cm below the soil surface. Both temperatures were measured using a glass mercury thermometer or a Reotemp, Inc. 60 cm metalprobe thermometer.

Snow and Litter Removal Experiment

A snow and litter removal experiment was conducted in the winter of 1977 to 1978 in order to determine the effects of exposure on overwintering shoots of *C. lacustris*. Fifteen 0.2 m^2 quadrats were randomly selected in fall 1977 at a control site and permanently marked with wooden stakes. All detached litter was removed from the quadrats by hand; all standing dead vegetation was clipped to an even height of 50 cm above the soil surface. Clipping closer to the soil surface would have removed or damaged live fall shoots. Shoot number, height, and condition were recorded for each permanent quadrat and for 15 randomly selected control quadrats in the same area. Snow was removed regularly, although not necessarily immediately, from the permanent quadrats throughout the winter. Removal was conducted by hand and with a soft brush to prevent physical damage to the shoots. Measures of shoot number, height, and condition were repeated in late April for the 15 permanent quadrats and 15 randomly selected control quadrats within the same area.

RESULTS

Selection of Species

Common cattail (*T. latifolia*) and the common sawgrass or lake sedge (*C. lacustris*) were selected for individual population study on the basis of species field response, species importance within the study area and in other wetland systems, and on the basis of feasibility. Results of field observations, literature surveys, and feasibility studies are discussed below.

Both species exhibited immediate and obvious response to leakage from the cooling lake. A *T. latifolia* stand within 25 m of the cooling lake dike remained green for several weeks after hard frost in fall 1975. Field observations in spring 1976 revealed that spring shoots failed to emerge or emerged sparsely. By mid-summer the stand appeared to have recovered.

However, mature plants remained green into early November, long after hard frosts. New shoots emerged in October. Many of these exhibited extreme chlorosis but retained turgor. Shoots of *C. lacustris* failed to emerge or emerged sparsely in spring 1976 in areas where it had been abundant the previous fall.

Both *T. latifolia* and *C. lacustris* are important species in the study area and in wetlands in general. *T. latifolia* is one of the most common and widely distributed wetland plants in the northern hemisphere (McNaughton 1974, Sculthorpe 1967, Fassett 1957). Although not widely distributed in the study area, it dominated localized areas where it did occur. By 1977, *Typha* had increased in abundance and distribution except within 50 m of the cooling lake. *C. lacustris* was abundant in five of six wetland communities on the Columbia site prior to impact. By 1976, it had been virtually eliminated in extensive sections of all communities. *C. lacustris* is common in wetlands of the prairie pothole regions (Steward and Kantrud 1972), the northeast (Bernard and MacDonald 1974), and the upper Midwest (Bedford et al. 1974, Swink 1974).

Both species are large, rhizomatous perennial species known to have large winter standing crops (Bernard and Bernard 1977, Gustafson 1976). The large size of rhizomes made collection and sorting of below-ground material feasible.

Both species have been studied extensively (Bernard and Gorham 1978, Auclair et al. 1973 and 1976, Gustafson 1976). Data were available on life history cycle, including seasonal patterns of shoot emergence, growth, and below- and above-ground biomass (Bernard 1975, Bernard and Bernard 1977, Bernard and MacDonald 1974, Bernard and Solsky 1977, Dykyjova et al. 1972, Fiala 1971, Gustafson 1976, Jervis 1969, Linde et al. 1976, McNaughton 1974). Additional information on seasonal patterns of carbohydrate storage and shoot phenology for Wisconsin populations was available for *T. latifolia* (Gustafson 1976, Linde et al. 1976).

Typha latifolia

Environmental Factors--

Sampling sites for *T. latifolia* covered a range of temperature and water level conditions. Temperatures in the rooting zone at the control site followed an expected seasonal pattern of winter freezing, spring and summer warming, a fall cooling (Figure 35). Substrate temperature patterns for sites west of the cooling lake varied in magnitude and seasonal distribution with distance from the lake. In general, magnitude and temporal patterns of temperature changes were attenuated with increasing distance from the lake. Water levels were continuously above the surface and fluctuated < 6 cm at all sites, but differed in mean value. Mean water level at the control site was 8.3 ± 5.4 cm (s.d.).

Area 03, located within 25 m of the west dike, exhibited the greatest temperature increase and departure from normal seasonal temperature patterns (Figure 36). Mean substrate temperature in January was $\sim 15°C$, i.e., 15°C

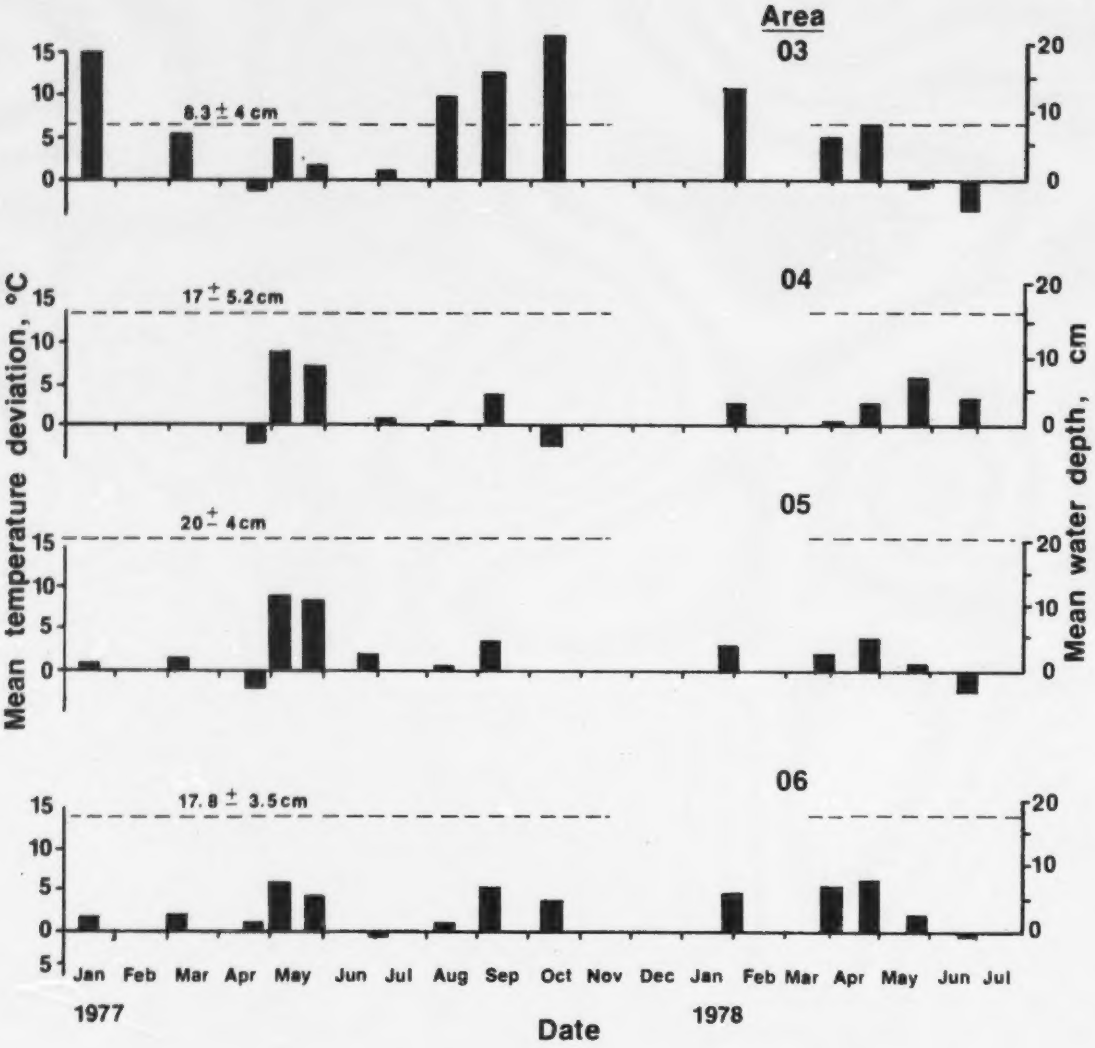

Figure 36. Temperature patterns in the substrate and mean water levels (± s.d.) for *Typha latifolia* sites. Note that temperature is represented as degrees above or below control site values.

above control site temperature. Late April substrate temperature fell to below control site temperature. Temperatures rose in late summer and fall to exceed control site temperatures by 11 to 17°C. Mean water level was 8.3 ± 4.0 cm (s.d.).

Area 04, located ∿ 350 m from the west dike, unexpectedly showed some temperature alterations (Figure 36). The site remained frozen throughout the winter but had late spring substrate temperatures 6.8°C above control site temperatures. Mean water level was 17.0 ± 5.2 cm (s.d.).

Although located ∿ 325 m from the west dike, Area 05 did not freeze in winter 1977 (Figure 36). High water flow kept the area open. Except for winter open water conditions, temperature patterns in Area 05 were similar to those in Area 04. Mean water level was 20.0 ± 4.0 cm (s.d.).

Area 06, ∿ 150 m west of the dike, experienced almost continuous slight temperature elevation (Figure 36). The area had open water conditions in January and early March, but substrate temperatures were < 2°C above control site freezing temperatures. The greatest temperature increase (∿ 5°C above control) occurred in early May. Mean water level was 17.8 ± 3.5 cm (s.d.). Rapid water movement through the area was evident throughout the year.

Carbohydrate Reserves--

Undisturbed sequence--Carbohydrate values in rhizomes of *T. latifolia* at the control site (Area 07) fell within expected seasonal values for undisturbed Wisconsin stands (Figure 37). The January 1977 mean at the control site compared closely to values reported by Gustafson (1976) and Linde et al. (1976) for south-central Wisconsin stands of *T. latifolia* at the end and beginning of the growing season. Gustafson obtained mean values for % TNC in cattail rhizomes of 45.0% in early April and 40.6% in early October. The October mean is the average of Gustafson's (1976) mean values for 1973 and 1974 rhizomes. Since rhizomes were not separated into age classes, Gustafson's values were averaged here and in Figures 37 and 38 for comparative purposes. Linde et al. (1976) reported similar though somewhat higher values for mid-April and late September. It was inferred that the value obtained at the control site (43.8%) reflects normal over-winter carbohydrate levels. The carbohydrate mean for the control site dropped as expected during spring shoot growth and rose again by the beginning of winter dormancy to a value (48.7%) close to those reported by Gustafson (1976) and Linde et al. (1976). The January 1978 mean for the control site (31.6%) is considerably lower than the 1977 mean, but well above seasonal low values. An unusually high proportion of old rhizomes and low number of *Typha* culms observed in the samples may explain the low value. Linde et al. (1976) reported that the lowest TNC storage occurred in the distal portion of old rhizomes, $\underset{-}{\sim}$ 33% compared to the January 1978 value of $\underset{-}{\sim}$ 32%. A fourth sample was dropped from calculation of the mean because it contained an unusually low biomass of rhizomes, > 95% of which were badly decayed. The randomly placed quadrat had contained no aboveground *Typha* culms. The control site initially and throughout the study had a lower density of aboveground shoots than all other stands. The probability of a randomly

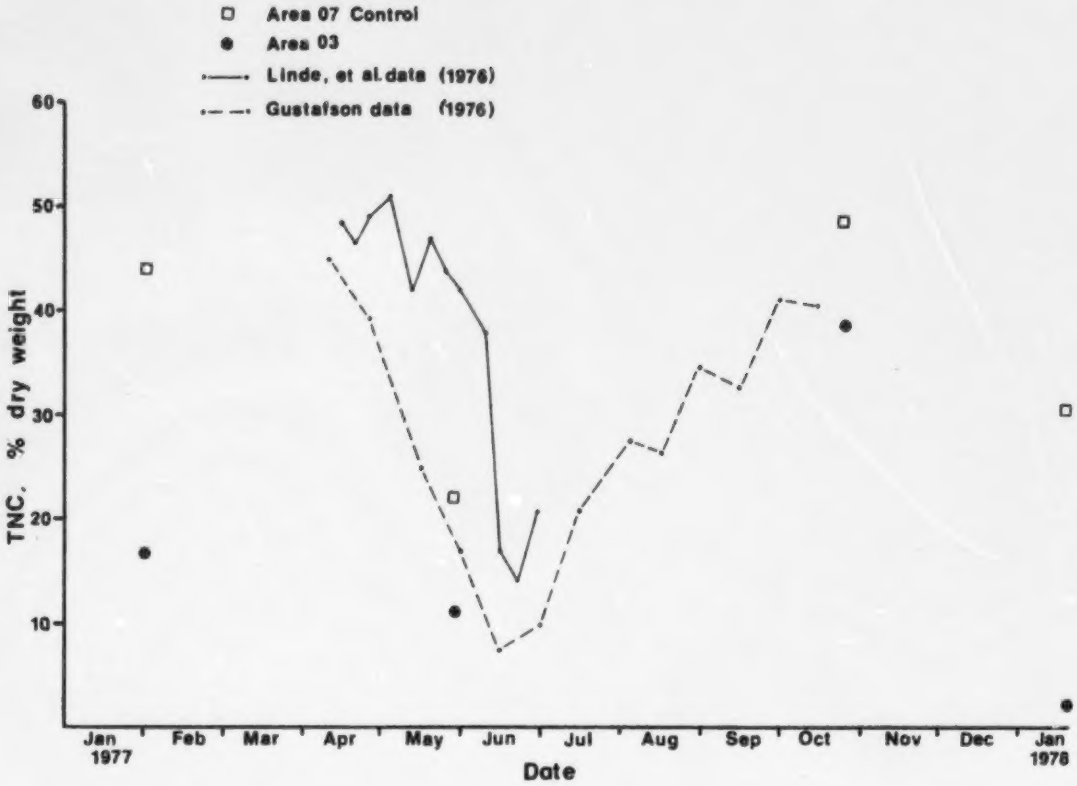

Figure 37. Seasonal changes in total nonstructural carbohydrates for the *Typha* control site (Area 07) and Area 03 compared with values reported in Linde et al. (1976) and Gustafson (1976).

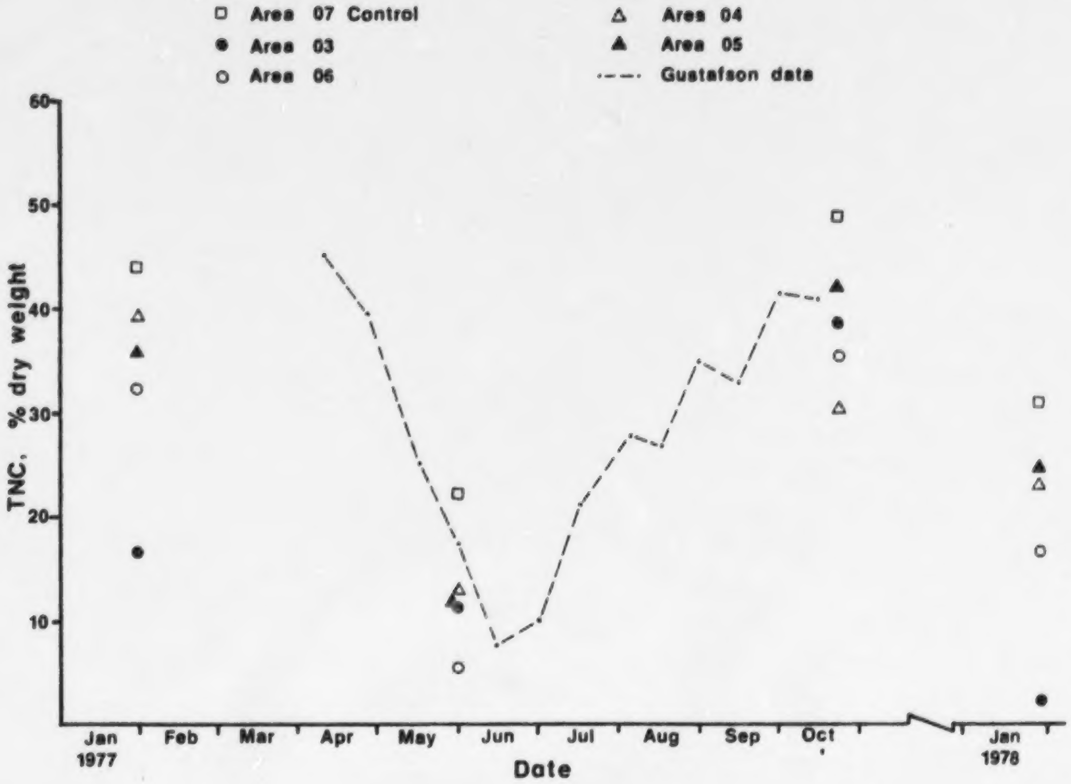

Figure 38. Seasonal changes in total nonstructural carbohydrates for the *Typha* control site (Area 07) and four other sites compared with Gustafson (1976).

placed quadrat falling between culms and the proximal portion of rhizomes, therefore, was higher than for other sites.

Response to waste heat in winter--Midwinter carbohydrate (% TNC) values for rhizomes of cattail plants subject to high winter temperatures were significantly lower than those for the control site (Figure 37). January 1977 TNC levels at Area 03, where mean substrate temperature was 15°C, approached the lowest levels reported by Gustafson (1976) and Linde et al. (1976) for the entire growing season. Such low levels normally are reached only during active growth when photosynthesis can compensate for respiration.

Rhizomes of plants in Areas 05 and 06 experienced only mildly elevated winter temperatures (1.4 and 1.8°C, respectively). January 1977 TNC levels were correspondingly lower than values for the control site and Area 04, which remained frozen. However, mean % TNC for both sites was well above storage values at Area 03 (Figure 38).

The hypothesis that warm winter temperatures result in low carbohydrate reserves is supported by the overall seasonal pattern of carbohydrate storage in Area 03 (Figure 37). October levels did not support an alternative hypothesis that warm summer temperatures result in low winter carbohydrate reserves by decreasing the summer production:respiration ratio. By late October, rhizomes in Area 03 contained 38.6% TNC, just below Gustafson's (1976) value of 40.1% for the same time of year in an undisturbed stand. Under warm fall and winter temperatures (Figure 36), TNC again dropped, this time to a mean of < 6% TNC.

The 1978 winter data for Areas 04, 05, and 06 also point to a direct relationship between groundwater temperatures and TNC deplection in *T. latifolia*. By 1978, substrate temperatures at these sites were warmer than 1977 temperatures. January 1978 TNC levels were correspondingly lower. The greatest depletion (excluding Area 03) occurred at Area 06 where temperatures were higher in fall and winter than at either Area 04 or 05. Although winter 1978 substrate temperatures in Area 06 ($\bar{X} = 4.8$°C) averaged only 3.0°C higher than 1977 values and < 2°C above Areas 04 and 05 in 1978, TNC levels were significantly lower than 1977 values and 1978 levels for Area 04 and 05. Since winter carbohydrate depletion is probably a function of cumulative temperature (Stewart and Bannister 1973), warmer temperatures in late fall after photosynthesis ceased and the early winter at Area 06 likely account for the differences.

The TNC values in *Typha* shoot bases followed patterns similar to rhizome patterns. The means and standard deviations for both are presented in Appendix B-1.

Response to other changes in temperature—Temperature increases during spring, summer, and fall, in the range observed at the sampling sites (1 to 13°C), apparently did not produce a negative effect overall on growing season TNC balances or account for decreased plant size or population number in *T. latifolia*. High May temperatures were correlated with significantly lower TNC levels than those at the control site, and plants at Columbia sites all had lower fall TNC values than the control site. However, three of the four sites (Areas 03, 05 and 06) showed a greater net increase from May to October than the control site. All sites accumulated ≥ 30% TNC in rhizomes by October (Figure 38) despite elevated spring temperatures, low spring TNC levels, and a range of temperature changes from May through October 1977 (Figure 36). Furthermore, *Typha* plants at Areas 04, 05, and 06 all attained apparently normal shoot height (Figure 39) and shoot density (Figure 40) during the 1977 growing season. Only Area 03, which was subject to winter temperatures ≥ 15°C, showed significantly reduced plant height and number by June 1978. (See below for data on shoot height and number).

Differences between sites in fall TNC values did not relate directly to fall groundwater temperatures. Differences may indicate the interaction of positive and negative effects of temperature on different plant processes at different times of the growing season. Fall carbohydrate levels in rhizomes represent a balance of photosynthesis, growth, respiration, and translocation processes throughout the growing season and monthly data on each of these varibles in lacking.

Responses to other environmental factors--Water level was not found to be a critical variable in *Typha* carbohydrate storage in the study area. *T. latifolia* is a known hydrophytic species which does well in shallow water and under continuously flooded conditions (Linde et al. 1976, Sculthorpe 1967). Mean water level increases on the Columbia site were small (∼10 cm). Three of the sites had nearly equal mean water depths and the fourth differed by only 10 cm. All values were within the favorable range for cattail.

It cannot be concluded from the TNC data that winter open water without increased temperature had a significant effect on carbohydrate storage in *Typha*. Area 05, which was in all other ways similar to Area 04, did not have significantly different TNC levels except in October.

Plant Phenology--

Undisturbed sequence--Although formed below the soil surface, most *Typha* shoots usually do not emerge above the surface until spring (Bernard and Bernard 1977). After initial shoot emergence in April to early May, shoot numbers stay fairly constant through out the growing season (Gustafson 1976). Shoots elongate rapidly sometime during late April to late May, after which their height increases steadily through mid-July. Mean height remains at or about this value until senescence (Gustafson 1976, Linde et al. 1976). *Typha* shoots in the control area for this study generally followed this pattern.

Response to waste heat in winter--*Typha* shoots emerged early in Area 03, where January and March temperatures were significantly above the frozen conditions at the control site (Figure 36) (See Figure 48). Shoot density decreased with onset of the growing season. Apparently the reported low January carbohydrate levels were insufficient to support spring shoot emergence and growth. By mid-May, the stand had not attained a shoot density comparable to the previous season's density, the control site, or

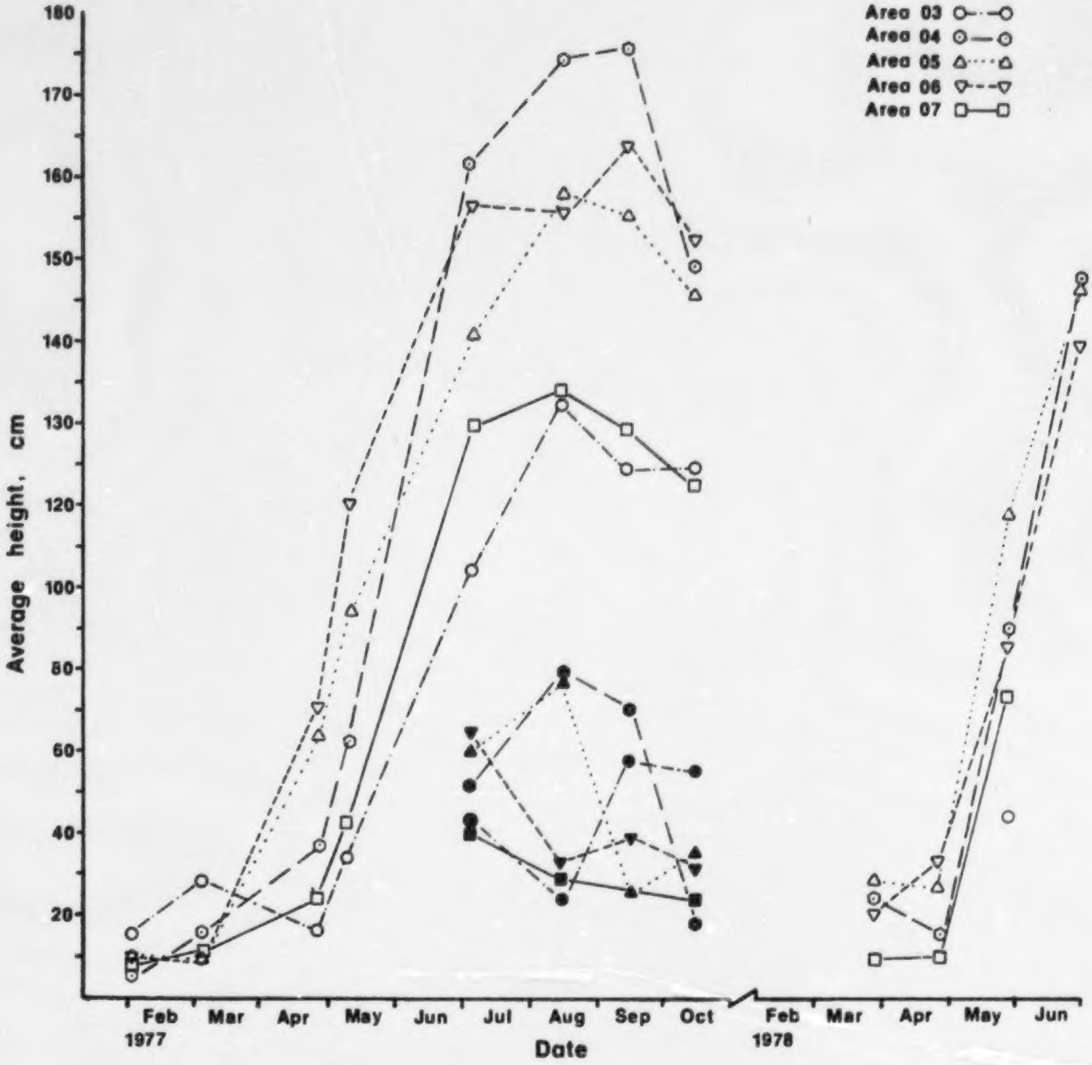

Figure 39. Average height (cm) of *Typha latifolia* shoots at control and four other sites. Closed symbols show heights of newly emerged shoots.

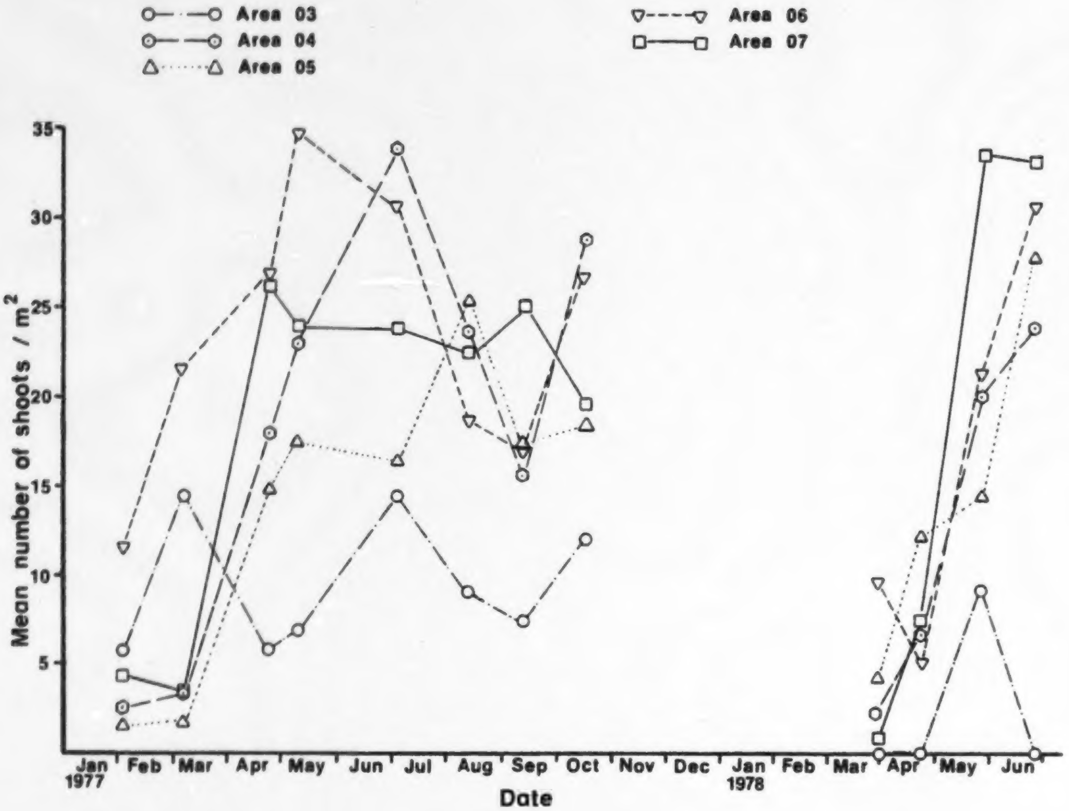

Figure 40. Seasonal changes in shoot density (mean number of shoots/ quadrat) for *Typha latifolia* at control and four other sites.

other sampling areas. Shoot number fluctuated throughout the growing season but never exceeded the number of shoots present in early March. Although the October rhizomes of these plants contained near normal TNC concentrations, high winter temperatures reduced TNC levels to < 3% by January 1978. Only a few shoots emerged late in May 1978. Shoot number dropped to zero by the end of June.

Responses to other changes in temperature--Temperature increases of < 10°C during the growing season did not result in extensive chlorosis, reduced plant size, or shoot mortality in *T. latifolia*. Elevated spring and fall temperatures altered shoot phenology but did not reduce population density significantly during the sampling period reported here (Figure 40). Shoots in Areas 04, 05, and 06 tended to gain height more quickly in spring (Figure 39) and remain green later in fall (Figure 41) than did shoots at the control site. Other phenological changes included early spring shoot emergence and fall shoot emergence. In general, extensive chlorosis did not occur at these sites during the growing season. An unexplained decrease in shoot number at Areas 04 and 06 and an unexplained increase at Area 05 occurred from late June to mid-August (Figure 40). Otherwise, changes in shoot emergence, growth, and loss of chlorophyll generally were correlated with increased groundwater temperatures.

Typha shoots at all Columbia sampling sites remained greener longer in fall than did control site shoots. Significantly smaller proportions of shoots at all Columbia sites were > 80% chlorotic by 15 October 1977 than at the control area (Figure 41). Shoots closer to the west dike (Areas 03 and 06) were somewhat less chlorotic than shoots > 300 m from the dike (Areas 04 and 05).

The data contain minimal information on the effects of mid-summer temperature increases and below-normal temperatures. Significant changes in summer groundwater temperatures occurred only at Area 03, where the effects of high winter temperatures already were evident. High August temperatures at Area 03 were correlated with a drop in shoot number but the relationship between the two events is not clear. Shoot number also dropped from July to August at Areas 04 and 06 where temperature increases were minimal.

Below-normal groundwater temperatures occurred at some sites in late April, early July, and mid-October 1977 and in late May and June 1978 (Figure 36). Changes were < 3°C and no relationship to shoot phenology emerges from the present data analysis.

Response to other environmental factors--Changes in onset of shoot emergence and delayed dieback in *T. latifolia* do not appear to be correlated to water levels at the Columbia site. Different patterns of response were observed in sites with essentially the same mean water depth and variation.

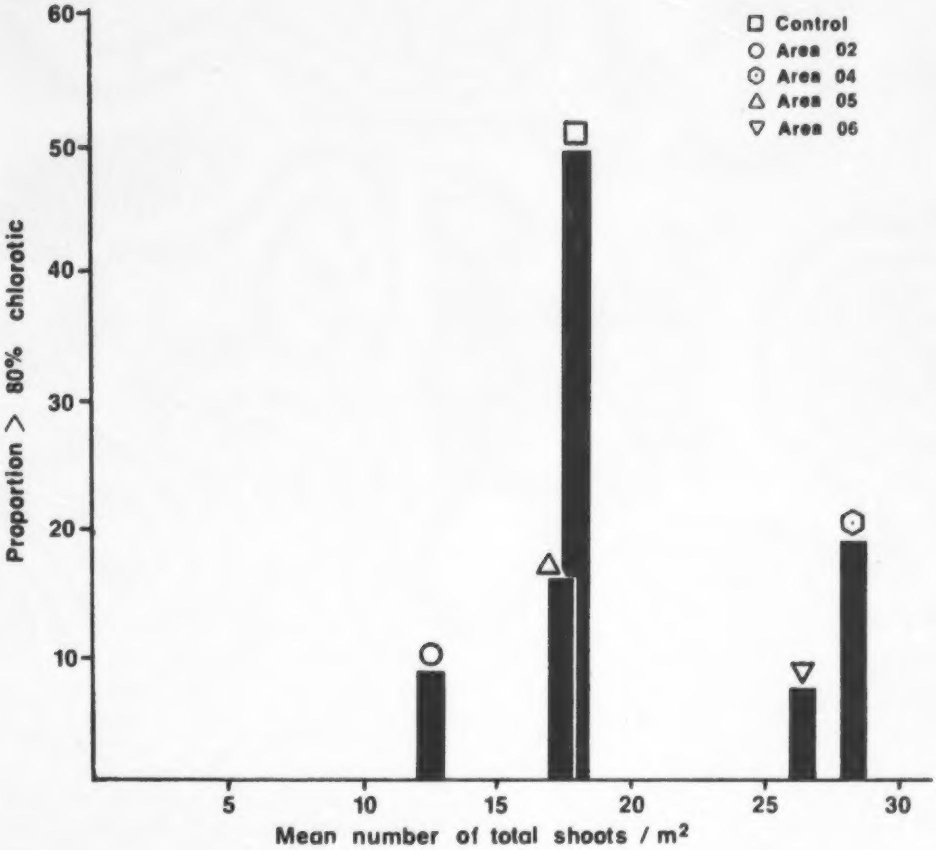

Figure 41. *Typha latifolia* shoots exhibiting >80% chlorosis on 15 October 1977 at control and four other sites.

Carex lacustris

Environmental Factors--

The range of conditions covered at the *C. lacustris* sampling sites was more limited than at the *Typha* sites because of the distribution of *C. lacustris* stands of adequate density and sampling area. Because appropriate stands were located near the cooling lake at distances ranging only from 25 to 50 m, all sites experienced temperature elevations in the range found at only one *Typha* site; differences between sites were minor in terms of the magnitude of these increases. Seasonal patterns, however, differed substantially due to the combined effect of distance and variation between sites in compostion and depth of subsurface materials. Because of the time lag introduced by movement of cooling lake water through underlying peats and clay of different depths, the time at which the rooting zone temperature reached maximum varied between sites by as much as 5 months. The most extreme differences between sites occurred in winter when substrate temperatures ranged from 0 to 16°C. Seasonal temperatures at the control site followed the expected pattern of winter freezing, spring and summer warming, and fall cooling (Figure 35).

All sites except the control experienced the same approximate increase in mean water level (10 cm) after the cooling lake was filled in the winter of 1974 to 1975. Although the new mean level differed from site to site, the range was $<$ 13 cm and all sites west of the cooling lake were subject to continuous soil saturation or flooding. Portions of the control site, with a mean level of 2.8 ± 2.7 cm (s.d.), were not saturated in late summer.

Areas 01, 02, and 09 all experienced temperature elevations of similar magnitude (Figure 42). Seasonal variation departed most markedly from normal seasonal patterns at Area 09. Substrate temperatures in Area 09 were highest in winter and lowest in mid-summer. Mean substrate temperature in January 1977 was $>$ 16°C above the control site's freezing conditions. July and August temperatures were nearly 4°C below control site values. Mean water depth also was greatest at Area 09 ($\bar{X}$ = 12.0 ± 5.2 cm (s.d.)).

Area 02 also exceeded control site substrate temperatures by $\sim$ 16°C. However, this value was not reached until May. January temperatures were only slightly above freezing. Temperature and continuous surface water flow kept the area from freezing throughout winter 1977. Mean winter level (9.6 ± 2.6 cm (s.d.)) was lower than that at Area 09.

Seasonal temperature variation in Area 01 was similar to Area 02, but the magnitudes of the temperature elevations were lower. Area 01 remained frozen through winter 1977. Mean water level was 3.1 ± 2.6 cm (s.d.).

Area 09 was located within 25 m of the west dike. Areas 01 and 02 were $\sim$ 50 m from the dike and located in the area of the marsh with the deepest peat deposits ($\sim$ 3 m). Area 09 was located in the area of shallowest peat deposits ($<$ 1 m) (Andrews 1976).

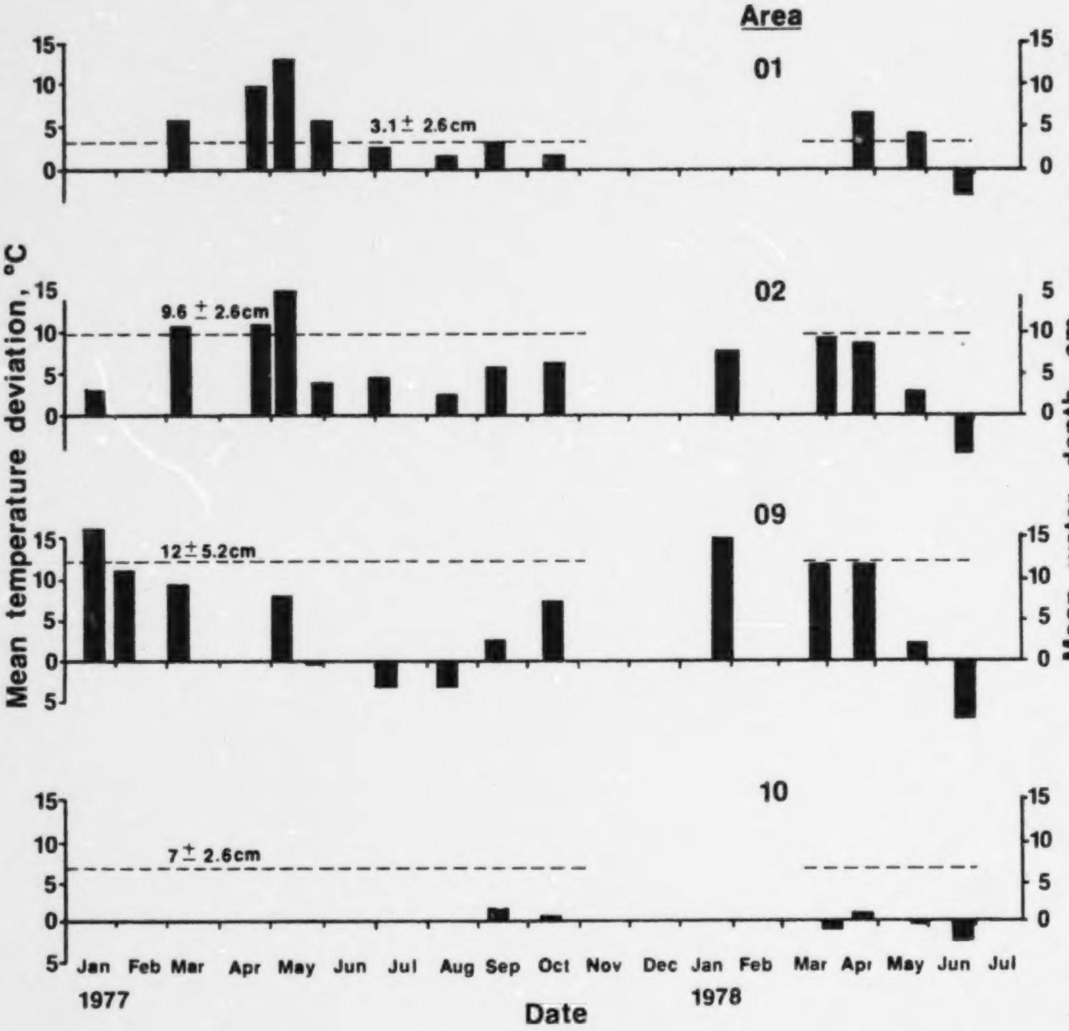

Figure 42. Temperature patterns in the substrate and mean water levels (± s.d.) for *Carex lacustris* sites. Note that temperature is represented as degrees above or below control site values.

Site 10 was added after the sampling program began when the limited range of conditions at sites 01, 02, and 09 became apparent. It had been excluded previously because of inadequate sampling area for repeated rhizome collections. Substrate temperatures at area 10 showed only minor departures from control site temperatures. Mean water level was 6.9 ± 2.6 cm (s.d.). It was located 60 m from the cooling lake.

Carbohydrate Reserves--

Undisturbed sequence--No data were available on seasonal carbohydrate patterns for *C. lacustris* at the time the study began. Bernard's (1974) biomass data for *C. lacustris* on seasonal contribution by rhizomes to total belowground biomass and on seasonal belowground biomass variation (Bernard and MacDonald 1974, Bernard and Bernard 1977) suggest a carbohydrate pattern similar to *Typha*. According to Bernard and Bernard (1977), *C. lacustris* has comparatively large winter standing crops, of which ∿ 70% is belowground; rhizomes represent at least 90% of belowground biomass throughout the year. Belowground standing crop is high in April, drops to a low in late May through July, and rises through late summer and fall to a January high.

Two important and related distinctions exist between the *Typha* and *C. lacustris* seasonal biomass patterns. A greater proportion of *C. lacustris* winter biomass is aboveground (30%) (Bernard and Bernard 1977) compared to 4% for *Typha*. Although both species form winter shoots, those of *Typha* usually remain at or below the soil surface. Most *C. lacustris* shoots overwinter as young, green shoots up to 50 cm above the soil surface (Bernard 1975, Bernard and MacDonald 1974, Bernard and Bernard 1977).

In 1979, Roseff and Bernard published data on seasonal carbohydrate changes in above- and below-ground tissues of *C. lacustris* (Figure 43). They found that TNC values reflected seasonal changes in biomass. TNC concentration in old rhizomes and roots was 29.2% in early May and declined to 22.1% by late June. By late October, TNC rose to a high of 44.9%. New rhizomes, which began growth in late June, followed in a similar pattern with one important exception: a low of 16.4% was reached in early August. Concentrations in live shoots averaged 18% throughout the year but varied for each of three cohorts. Until October, TNC in newly emerged shoots tended to be lower than in older shoots. TNC levels in shoots emerging before 16 July declined to between 3 and 4% by 5 December. Shoots emerging between 16 July and 19 September gained TNC through late October and maintained this level (16.1%) through 5 December.

Seasonal carbohydrate patterns of rhizomes at the *C. lacustris* control site (Figure 44) followed trends similar to Roseff and Bernard's (1979) data but at considerably lower levels. The lower concentrations can be attributed to differences in methods. Roseff and Bernard (1979), working in an undisturbed site, assessed TNC in 5 mg subsamples from healthy, entire rhizomes and roots. In this study, in order to compare values for disturbed and undisturbed sites, TNC was assessed in homogenized samples consisting of the mixture of healthy rhizomes and any recognizable pieces of rhizome, healthy or unhealthy, found in a given quadrat. The amount of

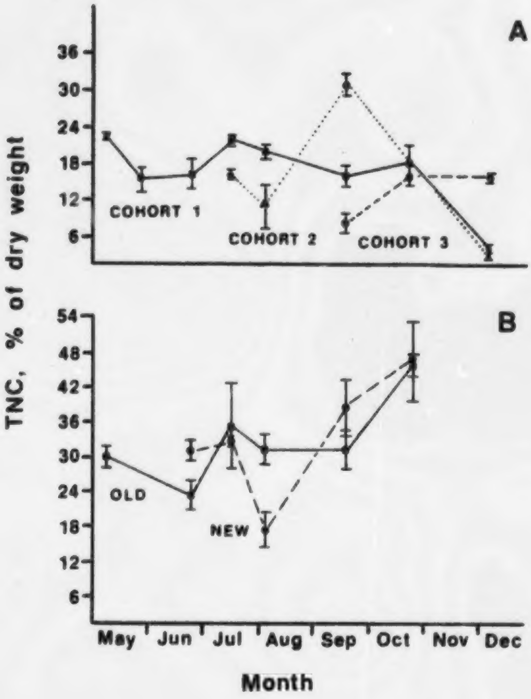

Figure 43. Seasonal changes in percentage of total nonstructural carbohydrates (± 1 S.E. indicated by vertical lines) in above-ground (A) and below-ground (B) tissues of *Carex lacustris* (from Roseff and Bernard 1979).

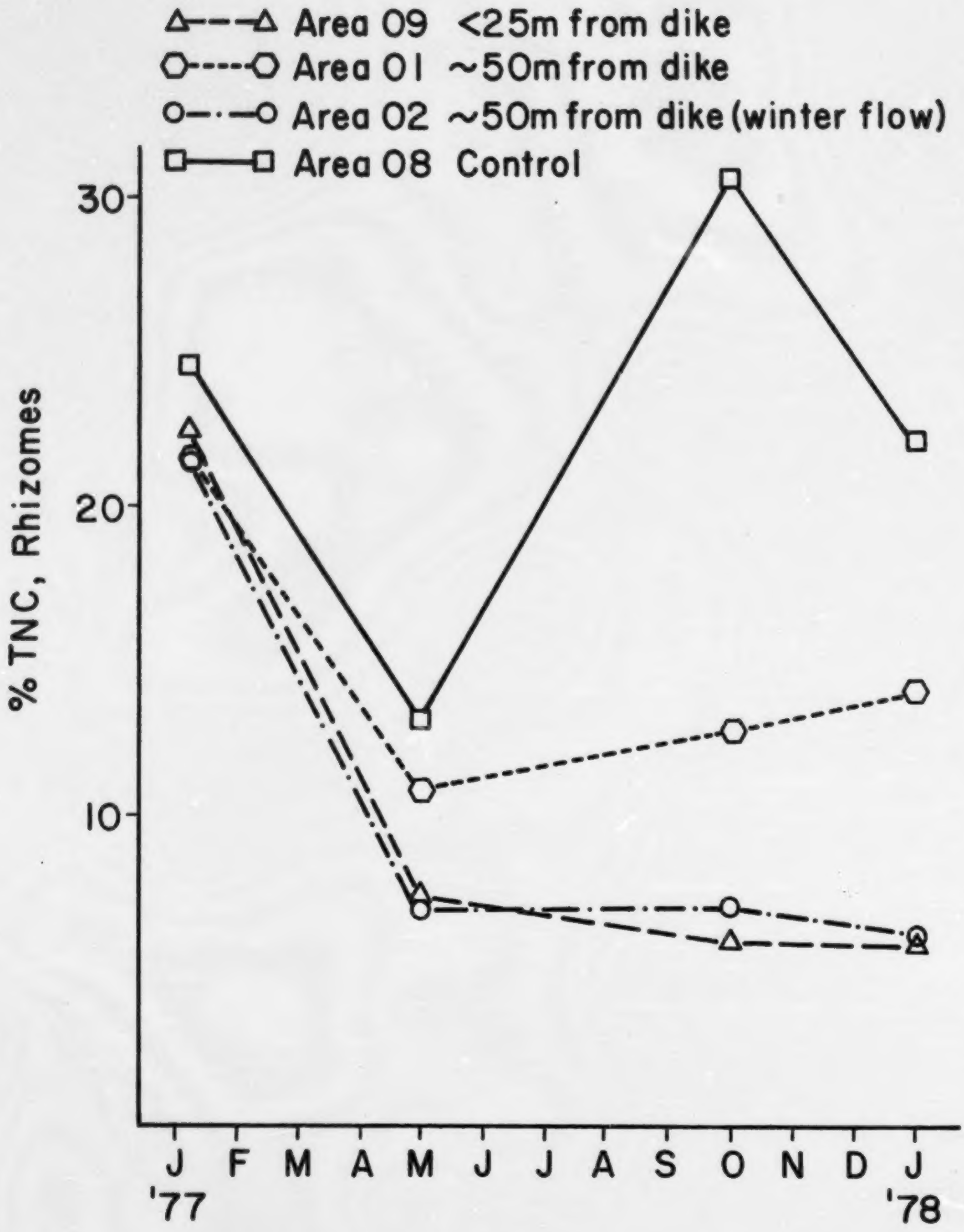

Figure 44. Seasonal changes in total nonstructural carbohydrates in rhizomes of *Carex lacustris* at control and three other sites.

non-carbohydrate biomass in the samples, therefore, was greater; the proportion of TNC in the total sample was lower.

Rhizome TNC data for the control site agreed with Roseff and Bernard's (1979) data in showing spring drawdown and fall build-up of reserves. Between May and October, TNC levels at the control site rose 18% to a high of 31% in late October compared with an increase of 15.7% to an October high of 45.4% for the New York population.

Seasonal carbohydrate levels in newly emerged (< 50 cm) shoots at the control site (see Figure B-2) varied little except in late May when concentrations dropped to a low of 2.8%. January 1977 (11.9%), October (11.6%), and January 1978 (11.4%) values were approximately equal.

TNC levels in aboveground tissues were measured only for newly emerged shoots. Comparisons with Roseff and Bernard's (1979) data are limited, therefore, to data for fall-emerging shoots. Shoots at the control site maintained approximately the same concentration (11.6%) from October to January, as did the New York population (16%), but at a somewhat lower level.

Response to waste heat in winter--January TNC levels in rhizomes of *C. lacustris* did not support the hypothesis that population decline occurred as a result of heat-induced exhaustion of winter carbohydrate reserves stored in underground organs. No significant differences existed between any of the sites for January 1977 TNC values despite differences in January 1977 temperatures covering more than a 16°C range (Figures 42 and 44). Furthermore, the May TNC data indicated that the sites showed only small differences in response to widely differing late-winter temperature patterns. By May, TNC levels at all sites including the control differed by < 6%. January 1978 values exhibited a pattern closer than January 1977 values to the expected response to temperature. However, this was not the result of temperature-induced depletion during winter 1977 to 1978. The TNC levels were low at the onset of winter. In fact, TNC concentrations changed little from May to January except at the control site. The lack of correspondence beween temperature and TNC levels in rhizomes indicates that winter groundwater temperatures did not act directly to deplete rhizome carbohydrates.

The higher proportion of winter biomass aboveground in *C. lacustris* than in *Typha* suggests that nonstructural carbohydrates stored in overwintering shoots might be more critical than rhizome carbohydrates. However, the data were inconclusive (see Figure B-2).

The TNC levels in overwintering shoots of *C. lacustris* were somewhat higher at Areas 09 and 02, which had open water, than they were at the control and Area 01, which remained frozen. Differences were not sufficient to explain spring shoot emergence patterns.

Responses to other changes in temperature--From May to October *C. lacustris* plants west of the cooling lake failed to build up carbohydrate reserves in rhizomes or shoot bases (Figures 44 and B-2). This does not appear to be the direct result of temperature changes during the 1977 growing season (Figure 42). The TNC patterns and temperature patterns during the 1977 growing season did not correspond to each other. Despite the fact that May groundwater temperatures at all sites west of the cooling lake were 7 to 16°C higher than at the control site. TNC levels were all within 6% of each other and the control site value. Temperature patterns from May to October 1977 were more similar between Areas 01 and 02 than between Areas 02 and 09. The TNC patterns from May to October were more similar between Areas 02 and 09 than between Areas 01 and 02.

On the basis of TNC and phenological data, the 1977 failure of *C. lacustris* to accumulate TNC in rhizomes and shoots seems to be the indirect result of temperature effects during the 1976 growing season and during winter 1976 to 1977 on aboveground shoots. The overall sequence of response suggests that reductions in aboveground photosynthetic material--e.g., number of individuals, size of individuals, and chlorophyll content--which had already occurred by May 1977 and continued through October, were the cause and not the result of low TNC levels in October 1977 and January 1978.

Postulations about the relationship between 1977 TNC patterns and temperature changes during the 1977 growing season can be inferred only from existing data. Monthly data on transpiration and photosynthesis rates are lacking. It is possible that high transpiration rates induced by elevated growing season temperatures exceeded photosynthetic capacity. However, the similarity in response between Areas 02 and 09 and the lack of correspondence between summer temperature patterns at these two sites do not support this hypothesis.

Response to other environmental factors--It is not possible on the basis of the short-term data collected to eliminate mean water level or continuous saturation of the soil surface as the important variables affecting carbohydrate levels in *C. lacustris*. Response to water level and seasonal fluctuation patterns is likely to be delayed (Bernard 1975, Mathiak 1971, Millar 1973) and act indirectly on carbohydrate levels.

It is inferred from the data that mean water level itself was not a critical factor in determining carbohydrate storage and depletion. This tentative conclusion is based on: 1. The two areas with most similar mean water depth (Control, $\bar{X} = 2.8 \pm 2.6$ cm (s.d.) and Area 01, $\bar{X} = 3.1 \pm 2.6$ cm (s.d.)) had widely divergent carbohydrate trends, and 2. TNC levels declined across a range of water depths ($\bar{X} = 3.1 \pm 2.6$ cm (s.d.) to $\bar{X} = 12.0 \pm 5.2$ cm (s.d.)). Furthermore, water levels at the onset of sampling were at equilibrium for 2 yr (Andrews and Anderson 1980).

Continuous soil saturation cannot be dismissed as a critical factor. All the Columbia sites were continuously saturated and, therefore, likely to be anaerobic. The control site probably experienced at least some periods when the soil was aerobic. The tolerance of *C. lacustris* to continually anaerobic sediments is not known. However, the persistence of *C. lacustris* in areas of the Columbia site that were saturated but not subject to either winter open water or elevated temperatures leads to the conclusion that continual saturation of the soil surface is not sufficient to produce the marked population decline of *C. lacustris* seen at the sampling sites.

Plant Phenology--

Undisturbed sequence--The life history strategy of *C. lacustris* differs markedly from that of *T. latifolia* according to Bernard and MacDonald (1974), Bernard (1975), Bernard and Bernard (1977), and Bernard and Solsky (1977) on New York populations. *C. lacustris* is unlike *Typha* in its seasonal patterns of shoot emergence, its extensive mortality during the growing season, and in the amount of living biomass aboveground in winter. Most of a given season's population emerges in fall of the previous year. These shoots overwinter, remaining < 50 cm in height, resume growth in April, and die in late autumn. Additional shoots may emerge in April and early May or after 1 July. Shoots which emerge before 1 October grow > 50 cm in height and die by winter. Most shoots emerging after 1 October do not grow > 50 cm and overwinter. However, as Bernard (1975) pointed out, "If some of the new shoots emerge early and grow too large, they also will die." How long shoots live depends on time of emergence.

Unlike the pattern shown for *Typha*, several different cohorts of *C. lactustris* shoots are present at any given time. Shoots emerge almost continuously throughout the growing season and considerable mortality occurs during the growing season. Total shoot number varies substantially with maximum total number reached in early fall. Since a substantial number of these fall shoots overwinter, aboveground winter biomass is higher proportionately than that of *Typha* whose shoots remain below the ground and emerge in spring (Bernard and Bernard 1977).

The sequence of shoot emergence and dieback observed at the control site (Figure 45) was similar to that reported by Bernard (1975) and Bernard and MacDonald (1974) in showing a major period of shoot emergence in fall, maximum shoot number in fall, substantial overwinter survival of fall-emerging shoots, and high growing season mortality. The sequence differed in showing two major periods of shoot emergence: one in fall--as Bernard (1975) reported--and another in May 1977 or April 1978. A greater difference between the number of fall shoots and the number or early spring shoots also was observed. This may be due to greater overwinter mortality in Wisconsin populations than in New York populations or may be an artifact of sampling dates and frequency. Bernard and MacDonald (1974) reported that of 344 live shoots/m^2 in late October of which $\sim$65% (225 shoots/m^2) were new shoots. The data in this study were comparable. Approximately 64% (149 shoots/m^2) of the total shoots alive at the control site in mid-October (232 shoots/m^2) were new shoots. However, by 1 April 1978 only 94 new shoots/m^2 were present. Bernard and MacDonald (1974) found 231 shoots/m^2 in late January. In other words, they found little or no mortality between October and January while at Columbia there was $\sim$40% mortality. Since Bernard and MacDonald (1974) did not report data for the following April, and since reliable shoot counts from January to 1 April 1978 were not completed at Columbia because of snow conditions, the reason for the greater mortality is not known. However, in 1977, 45% mortality occurred from late January to early March at the control site (Figure 45). This is comparable to the

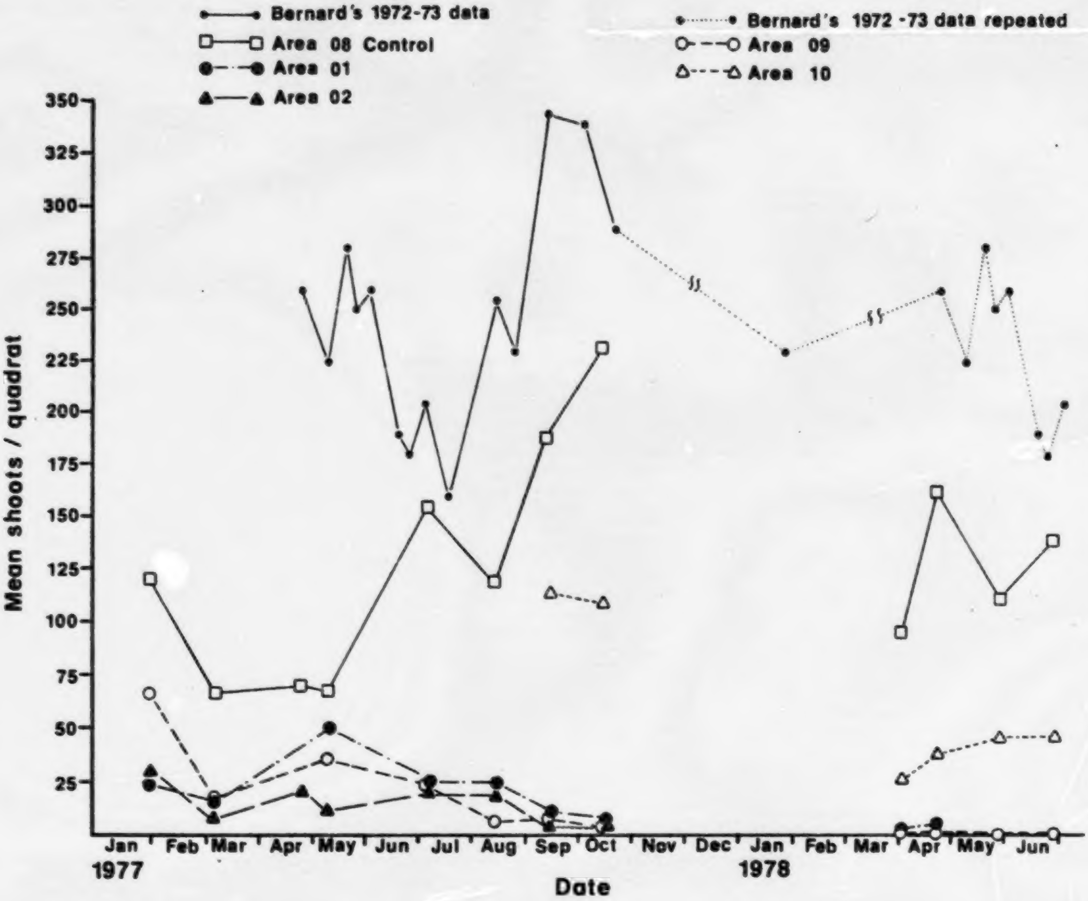

Figure 45. Seasonal changes in mean number of shoots/quadrat for *Carex lacustris* at mean control (Area 08) and three other sites compared with Bernard and MacDonald (1974).

October 1977 to April 1978 mortality rate and suggests that substantial overwinter mortality occurs in undisturbed Wisconsin populations.

Response to waste heat in winter--A substantial decrease in shoot number occured from late January to early March at the *C. lacustris* sites, including the control. However, areas subject to elevated winter temperatures (Areas 02 and 09) experienced greater proportional loss than did the control area and Area 01 which were frozen in January and February 1977. By early March, the control site and Area 01 lost 45 and 40% of shoots present at the end of January. Areas 02 and 09 lost 73 and 74%, respectively. Despite more than 10°C differences in January and February substrate temperatures at these sites, proportional losses were nearly equivalent.

Winter shoots tended to be somewhat taller at sites west of the cooling lake than at the control site (Figure 46). Differences in height were related more closely than shoot number to substrate temperature. Differences between the control and Areas 01 and 02 were insignificant in late January when temperatures were similar. March shoot heights were related directly to temperature; warmer sites contained taller shoots.

Winter shoots at sites west of the cooling lake were significantly more chlorotic than shoots at the control site (Figure 47). Like height, extent of chlorosis was related directly to substrate temperature. Shoots at Area 09, which showed the greatest departure from seasonal temperature patterns, were significantly more chlorotic than shoots at any other site. Early March shoots were almost completely chlorotic. Shoots at the control site exhibited only minor chlorosis. Shoots at Areas 01 and 02, where temperatures were intermediate between the control and Area 09, showed intermediate chlorosis.

The relationship between winter groundwater temperatures, winter air temperatures, shoot height, and chlorosis is not clear. Results of the snow and litter removal experiment showed that winter exposure alone produced extensive chlorosis in aboveground shoots. Winter exposure of shoots that were not subject to elevated groundwater temperatures resulted in significantly higher chlorosis than in nearby shoots protected by litter and snow (Figure 48). Exposed shoots also tended to be taller. Of those shoots that were exposed, chlorosis was greater in the taller height classes.

Response to other temperature changes--Departures from normal phenological patterns continued to occur at sites west of the cooling lake in spring, summer, and fall 1977. Shoot number increased from March to May in Areas 01, 02, and 09 while remaining constant at the control site (Figure 45). Spring shoots tended to be taller and more chlorotic at sites west of the cooling lake (Figures 46 and 47). From May to September shoot number showed a net increase at the control site but dropped at all other sites. Mature shoots in Areas 01, 02, and 09 were significantly shorter than shoots at the control site (Figure 46).

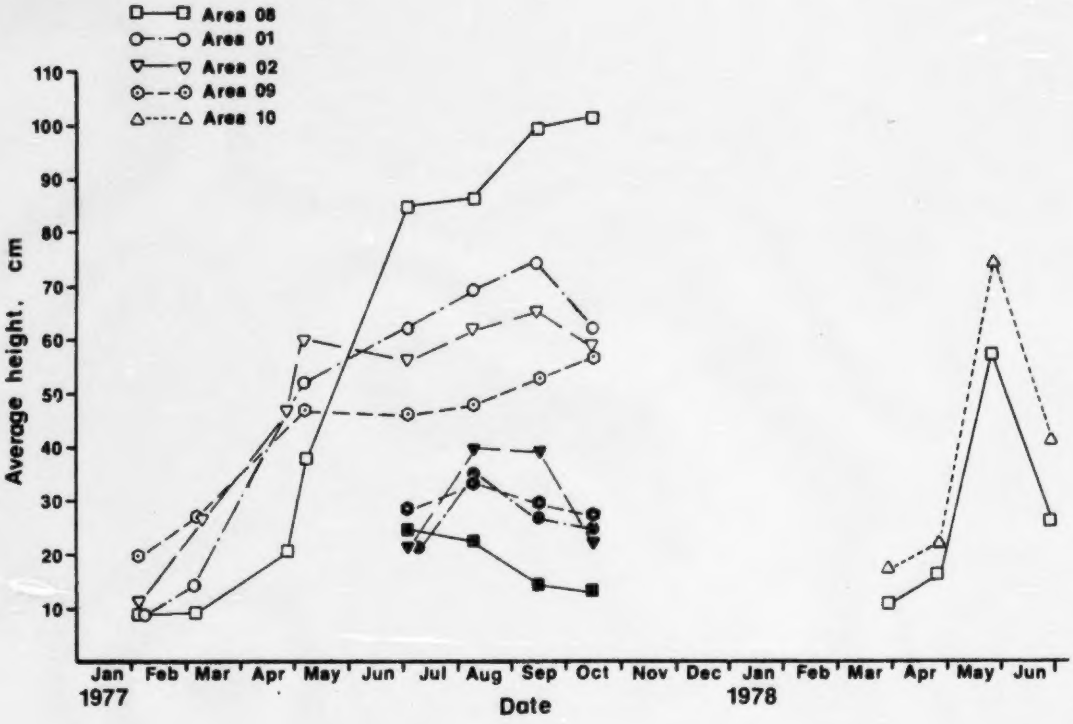

Figure 46. Seasonal changes in average height (cm) of *Carex lacustris* shoots at a control (Area 08) and three other sites. Closed symbols show heights of shoots ≤ 50 cm at time of sampling.

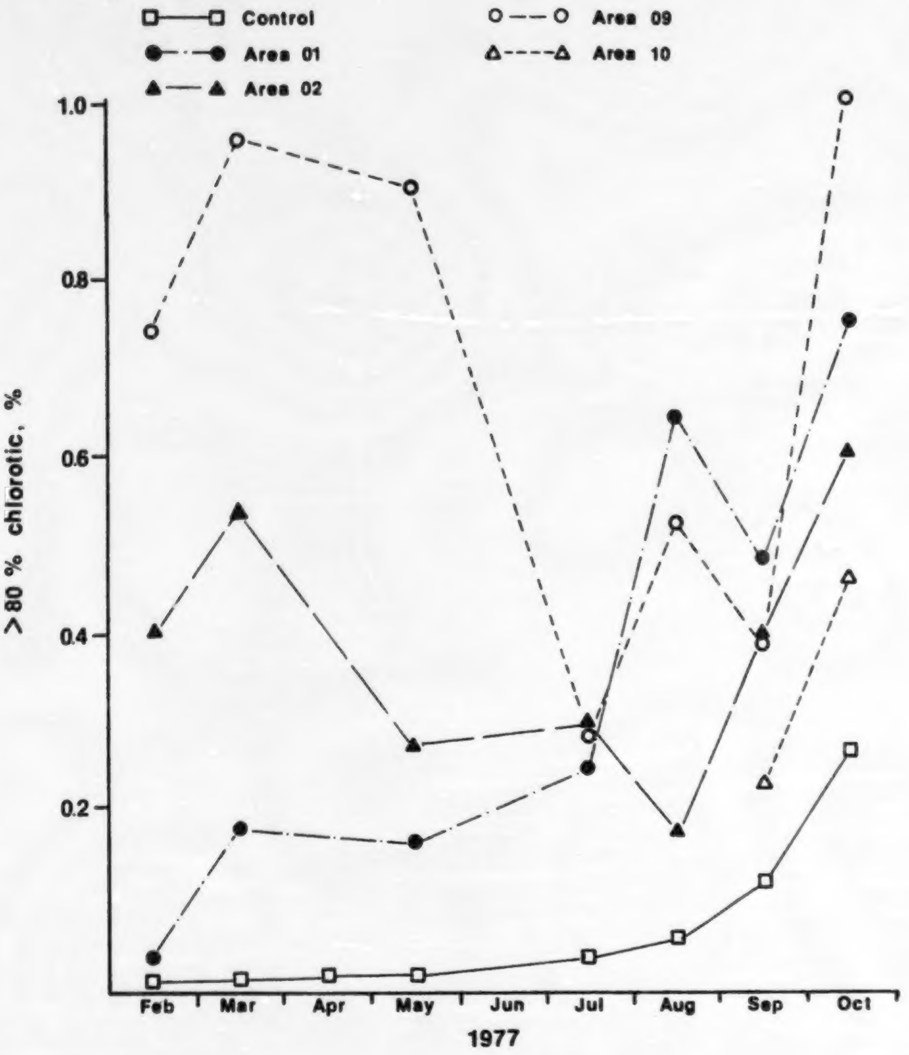

Figure 47. Seasonal changes in *Carex lacustris* shoots exhibiting >80% chlorosis.

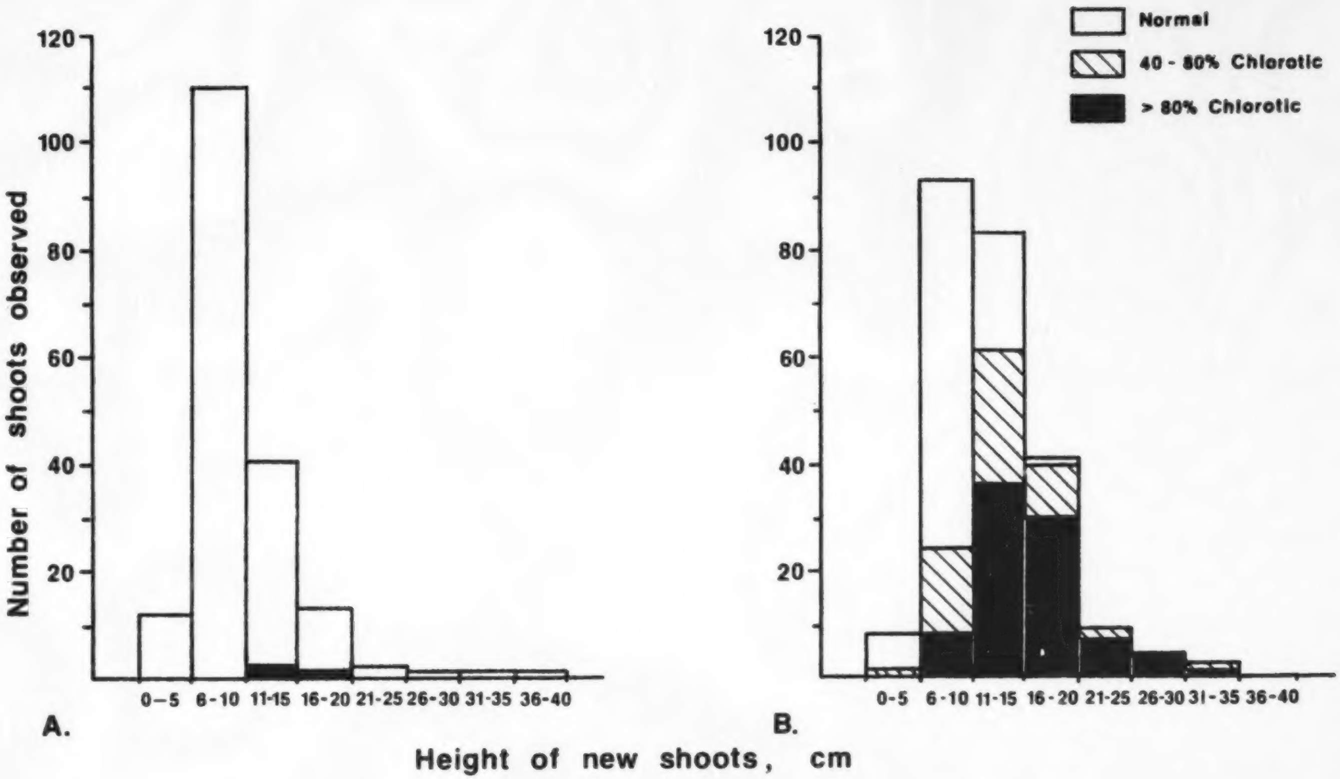

Figure 48. Number of *Carex lacustris* shoots exhibiting various degrees of chlorosis for different size classes: (A) control area; (B) experimental area with snow and litter removed.

Fall shoots failed to emerge at all sites west of the cooling lake. Remaining shoots were significantly more chlorotic than those at the control site.

By winter 1977 it was clear that *C. lacustris* populations had collapsed at all sampling sites west of the cooling lake. Populations did not recover the following spring.

In general, differences between sites in shoot number and height cannot be explained on the basis of carbohydrate levels in rhizomes or shoots and shoot bases. Only the failure of the fall 1977 cohort to emerge can be correlated to TNC levels. Since the population was already severely depleted by July 1977, it seems more likely that low October TNC levels were the result rather than the cause of low shoot numbers.

The entire sequence of data indicates that winter conditions alone do not account for the decline of *C. lacustris*. Instead of a single critical response period related to carbohydrate reserves--as seen for *T. latifolia*--*C. lacustris* showed continuous departure from normal phenological patterns; excessive winter mortality, increased spring emergence, summer decline in shoot number, no fall shoot emergence, extremely high spring and fall chlorosis, and taller new shoots but shorter mature shoots than at the control site. However, the 1977 and 1978 data sets reveal only part of the response sequence. Field observations and 1974 to 1977 survey data indicated that population density had already been decreased when sampling began in January 1977. Therefore, the effects of elevated spring, summer, and fall groundwater temperatures on a healthy population could not be quantified.

Data from Area 10 contributed additional--though incomplete information--on the potential effect of elevated groundwater temperatures on fall shoots in an undepleted population. The size-class structure of the *C. lacustris* population at Area 10 (Figures 49 and 50) indicates that minor temperature changes can alter shoot emergence and growth patterns. September and October substrate temperatures at Area 10 were only slightly above control site values (Figure 42). A greater proportion of shoots at Area 10 were in intermediate size classes (21 to 80 cm) and a smaller proportion in shorter size classes (0 to 20 cm) than at the control site. The average height in September of new shoots at Area 10 was 28.1 ± 25.1 cm (s.d.) compared to 14.6 ± 18.9 cm (s.d.) at the control site. Total shoot number in Area 10 dropped rather than increased from September to October. Overwinter mortality was 16% higher than in the control area.

Data from Area 10--taken together with the 1975 increase in fall shoot number observed in the area of major impact prior to the extreme drop in 1976 (Figure 15)--suggest that warmer than usual late summer and early fall substrate temperatures may induce early emergence and growth of fall shoots. Such alterations in normal phenological patterns could reduce population numbers in three ways. As pointed out by Bernard (1975), shoot life depends on time of emergence. If fall shoots that would otherwise overwinter emerge early or grow too tall, they die some time before winter. Overwinter mortality may be somewhat higher for taller shoots

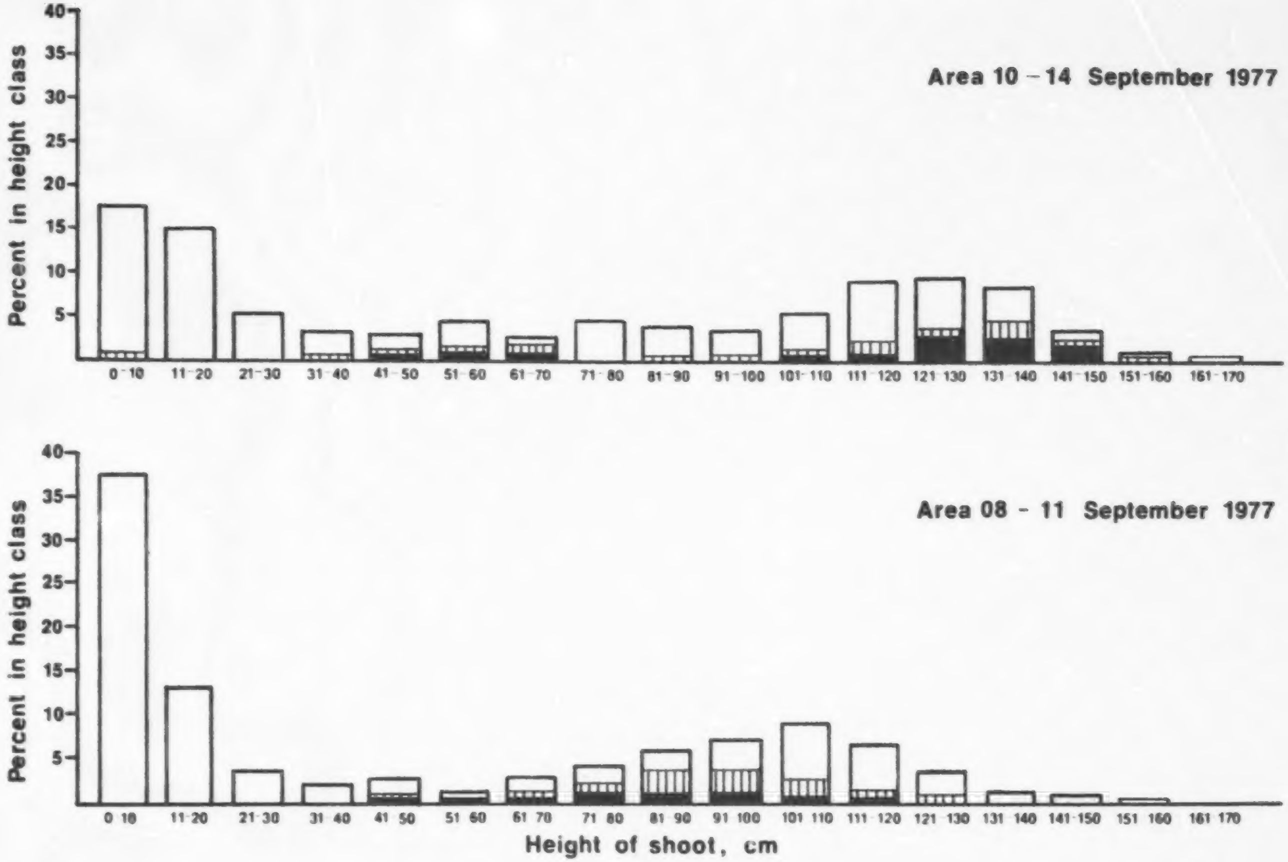

Figure 49. The fall size-class structure of the *Carex lacustris* population at Area 10 compared to the control site (Area 08) populations (September 1977).

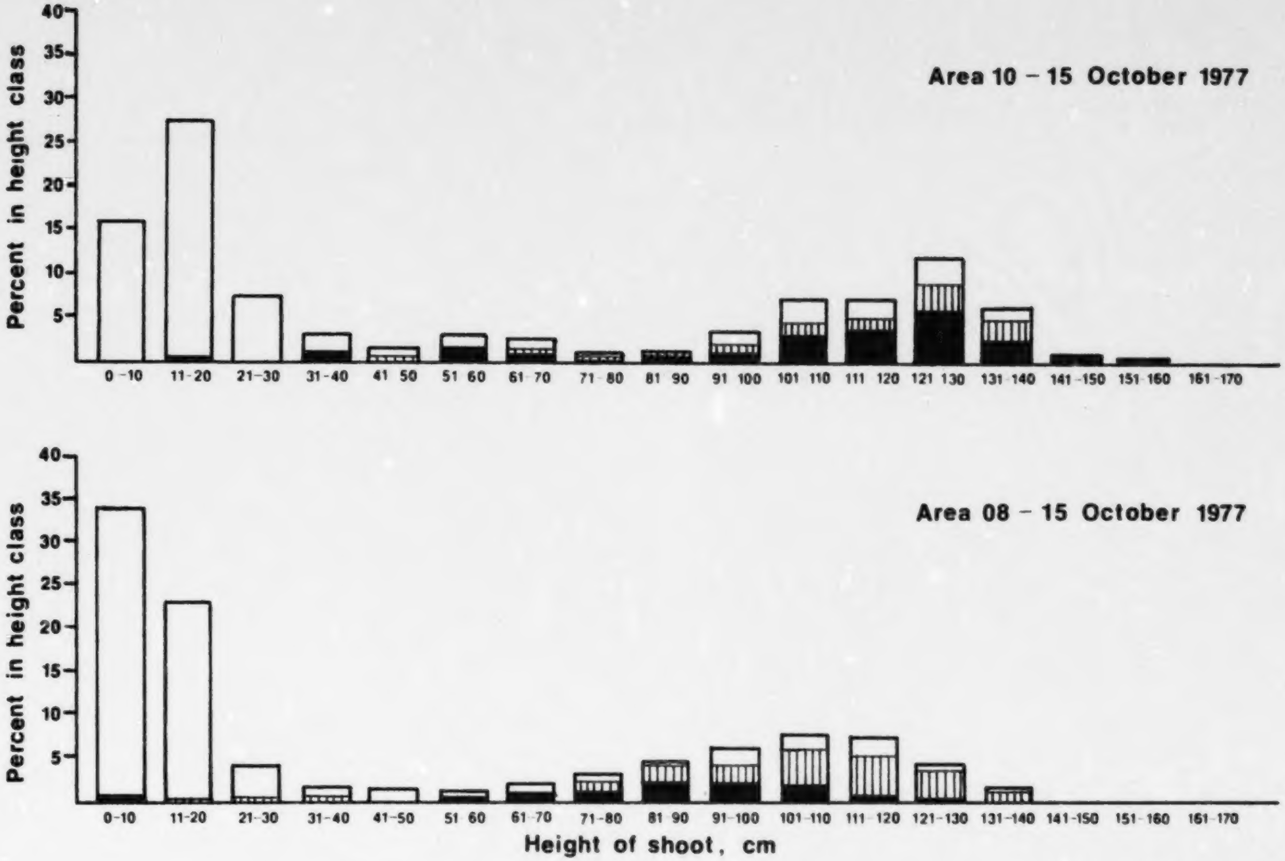

Figure 50. The fall size-class structure of the *Carex lacustris* population at Area 10 compared to the control site (Area 08) populations (October 1977).

exposed aboveground to winter air temperatures. Exposure-induced chlorosis in overwintering shoots combined with high fall and winter mortality may reduce the population's overall photosynthetic capacity to the point where it is insufficient to support growth, carbohydrate build-up during the growing season, or fall shoot emergence.

The response of *C. lacustris* cannot be attributed to a single critical period or mechanism. Differences between *C. lacustris* sites in shoot number cannot be explained on the basis of prevailing winter substrate tempratures or TNC levels in rhizomes and shoots. Although the data analysis is not conclusive, it seems that population decline in *C. lacustris* occurred as a result of the combined effects of continuously altered timing of shoot emergence and growth during the previous growing season (1976) and greater than normal overwinter mortality.

Response to other environmental factors--Although increased water levels, high surface water flow, and continous soil saturation probably contributed to the decline of *C. lacustris*, the departures from undisturbed seasonal patterns of shoot emergence, growth, and dieback seen at all sampling sites cannot be attributed to these factors. Several pieces of evidence from Areas 01, 02, 09, and 10 suggest this conclusion. Area 10 showed only minor changes in phenology and population density by spring 1978 despite a mean water depth (7.0 ± 2.6 cm (s.d.)) greater than that at Area 01 (3.1 ± 2.6 cm (s.d.)). Both sites were continuously saturated since 1975. Area 01 showed major phenological changes by spring 1977. Area 01 and the control site differed by < 0.5 cm in mean water depth and monthly variation. Water levels at all sites were below levels at which *C. lacustris* is known to survive (Auclair et al. 1973, Stewart and Kantrud 1972, Bernard, personal communication). Harris and Marshall (1963) reported that 4 yr of continuous flooding to depths of 15.2 cm were necessary to eliminate three species of sedges, including *C. lacustris*. *C. lacustris* was eliminated in 3 yr in < 4 cm of water at Area 01 and < 10 cm at Area 02. Finally, Area 01 was not subject to surface water flow but showed phenological changes similar to those seen in areas of high surface flow.

Changes in water level and flow likely contributed to the decline of *C. lacustris* in three ways. First, in limited, deeper areas of the marsh such as the emergent community, the small increase in mean level may have exceeded the tolerance range of the species. Second, higher water levels may have caused higher mortality during the growing season by increasing the proportion of flowering shoots in the population. Bernard (1975) related increased flowering to elevated water levels the previous year and reported that "the amount of shoot mortality during the growing season depends to a considerable extent on the number of shoots that flower." Third, increased flow was sufficient in some parts of the marsh to prevent winter freezing and to remove plant litter. Even without elevated groundwater temperatures these factors could contribute to population decline by increasing exposure of overwintering shoots. High surface flow also could alter phenological patterns through earlier warming of the sediments in spring. Nonetheless, the persistence of *C. lacustris* in areas that did not experience elevated groundwater temperatures but that were subject to continous flooding or saturation of the soil surface eliminates water level and soil saturation as critical variables regulating the response of this species to leakage from the Columbia cooling lake. The decline of *C. lacustris* at Area 01--where no surface flow occurred--eliminates surface flow as a single controlling variable.

Data from Areas 01, 02, 09, and 10 did not permit the relative contribution of hydrologic factors to be separated from the role of waste heat in the collapse of *C. lacustris* populations. Increased substrate temperatures, elevated water levels, and high surface water flow are directly related to increased groundwater discharge and are not independent. Near the cooling lake, where the heat has not dissipated, these factors tend to be interrelated. Areas 01, 02, 09, and 10 all were located within 60 m of the west dike of the lake.

DISCUSSION AND CONCLUSIONS

T. latifolia and *C. lacustris* fit the general hypothesis attributing population decline to heat-induced variations in plant phenology and plant metabolism. *C. lacustris* did not fit the specific hypothesis in regard to the regulating mechanism or sequence of response. Elevated temperature patterns resulted in population decline through continuously altered shoot phenology rather than through winter depletion of carbohydrate reserves as in *T. latifolia*. Furthermore, *C. lacustris* exhibited a greater sensitivity to stress. The phenological data, population data, and field observations showed that the magnitude of effect produced in *C. lacustris* by the various levels of waste heat and elevated groundwater levels was greater than for *T. latifolia*. Population data (section 3) showed an almost uniformly negative response by *C. lacustris* but positive and negative responses by *T. latifolia*. Typha exhibited a clear positive response to elevated water levels, increasing its density where it had been abundant and expanding its distribution substantially by 1977 (Figures 51 and 52). Adverse effects on *Typha* were restricted to areas where temperature increases were $>$ 7 to 16°C and occurred in winter. Viable populations of *C. lacustris* persisted only in areas where temperature increases were negligible throughout the year (Figure 53).

Information on specific field signs of heat stress and general species characteristics that may be useful indicators of potential sensitivity to stress can be inferred from interspecific differences and similarities observed in the response patterns of *C. lacustris* and *T. latifolia*. Similarities observed in the negative responses of both species identify field charactersitics that can be used as specific signs for detecting and monitoring heat stress in wetland plants. Interspecific differences in regulating mechanisms, sequences, and magnitude of response suggest species characteristics that might be generalized to serve as criteria for assessing potential sensitivity or physiological limitations of wetland plants to the combined effects of waste heat and elevated groundwater levels. However, the data must be interpreted cautiously and considered together with population data and field observations. Collection of the data reported here did not begin until January 1977, 9 months after field observations revealed extensive mortality of *C. lacustris* and altered timing of shoot emergence in *C. lacustris* and *T. latifolia*. Comparisons between the two

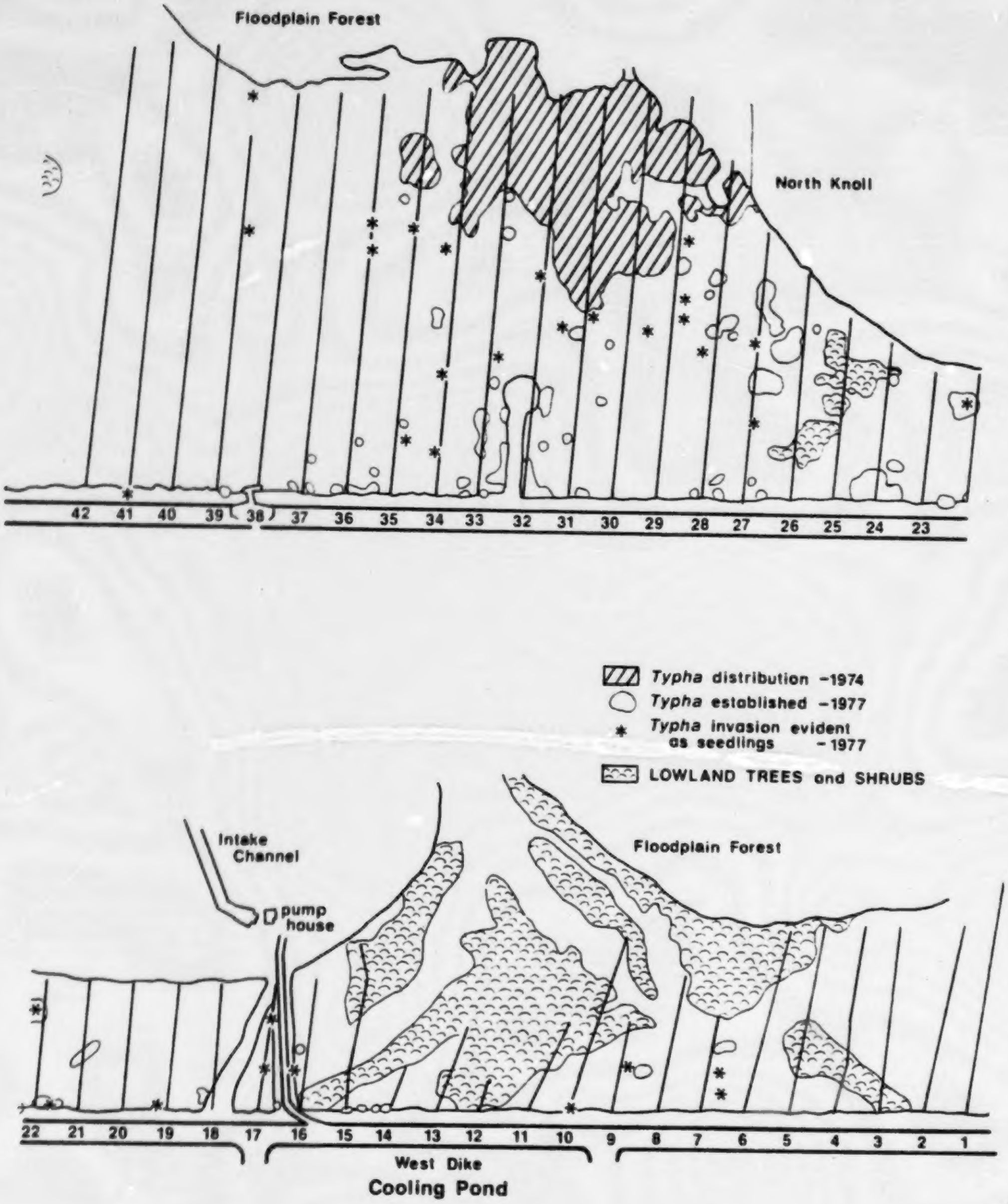
Floodplain Forest
North Knoll
42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23
Typha distribution -1974
Typha established -1977
Typha invasion evident as seedlings -1977
LOWLAND TREES and SHRUBS
Intake Channel
pump house
Floodplain Forest
22 21 20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
West Dike
Cooling Pond

Figure 51. Expanding distributions of *Typha latifolia* between 1974 and 1977.

Figure 52. *Typha latifolia* in 1977 invading areas of the Columbia marsh which *Carex* previously dominated.

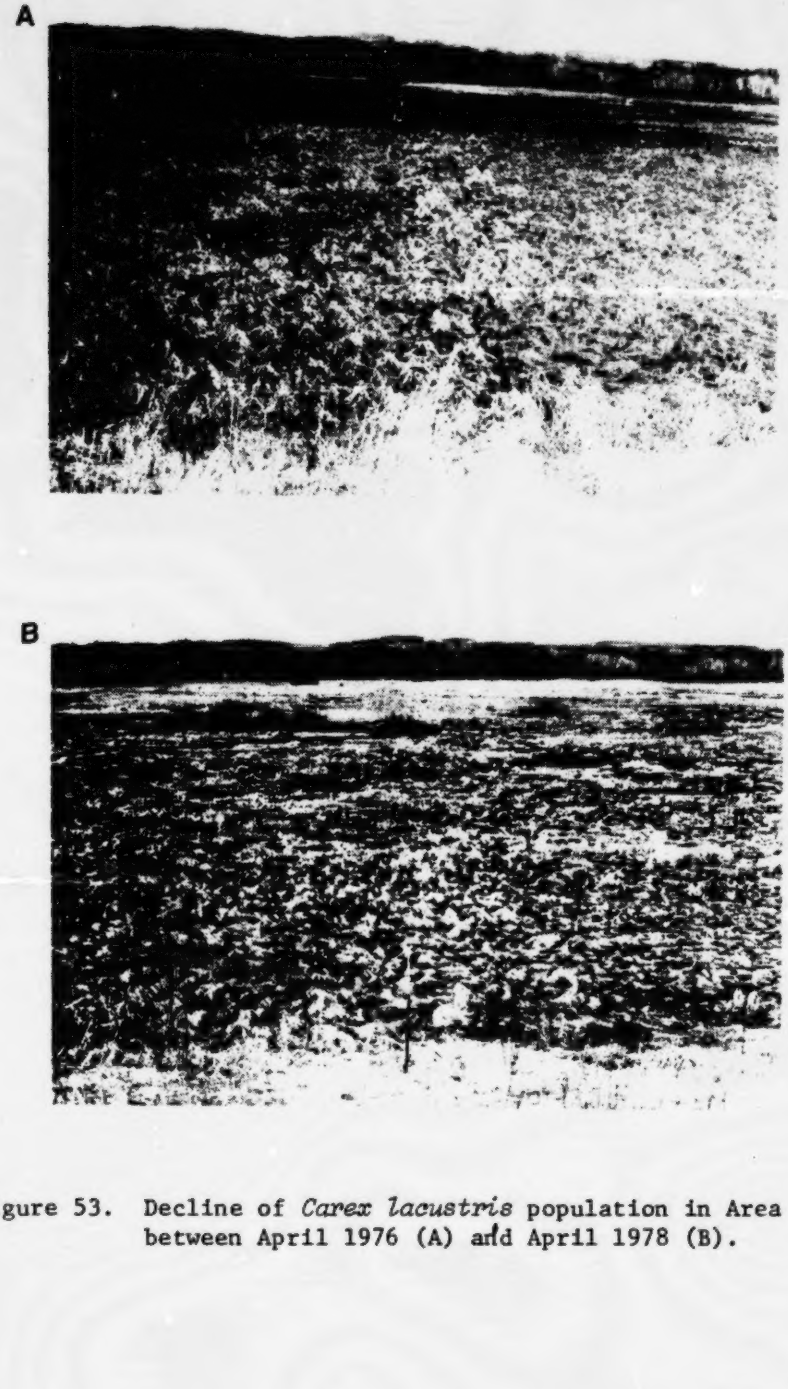

Figure 53. Decline of *Carex lacustris* population in Area 01 between April 1976 (A) and April 1978 (B).

species are constrained by the fact that sampling sites for *Typha* covered a wider range of temperature changes than did *Carex* sites. Although seasonal patterns differed among the *Carex* sites, no site experienced a temperature maximum < 14°C above the control site temperatures. Furthermore, the data do not include measures of the seasonal redox status of the sediments. The positive response of *Typha* probably is related to its tolerance of anaerobic conditions.

Phenological changes appear to be reliable indicators of heat stress (Figure 54). Although changes in population density occurred throughout the study area, phenological changes were not observed outside the area affected by altered temperature patterns. In areas receiving waste heat, individual plants showed visible signs of stress before the population collapsed. Where the species grew in dense stands, the symptoms were visible to the naked eye at distances up to 300 m. In general, phenological changes become evident 1 yr before population density was reduced and 2 yr before the population collapsed. Vadas et al. (1976) reported similar changes for Maine populations of *Spartina alterniflora* receiving waste heat.

Charactersitics of plants experiencing heat stress that were observable and easily measured in the field included: 1. Unseasonable chlorosis, 2. reduced height of mature shoots, 3. increased height of new shoots, and 4. early or delayed shoot emergence at reduced density. These phenological changes were evident in *C. lacustris* throughout the year. Extensive chlorosis did not occur in *T. latifolia* during the growing season. In general, phenological changes were more pronounced in *C. lacustris*.

Different phenological changes, which did not lead to reduced population density, were observed at *Typha* sites experiencing lower temperature increases and negligible winter increases. They included: 1. Early spring shoot emergence at previous densities, 2. rapid gain in shoot height during spring elongation, and 3. delayed loss of chlorophyll in fall. No negative consequences to the populations were evident by June 1978. Temperature increases up to 7°C in spring, summer, and fall appeared merely to extend the effective growing season for *T. latifolia*. The data suggest a subsidy effect rather than a stress (Odum et al. 1979).

The greater magnitude of effect observed in *C. lacustris* appears to be related to its particular life history characteristics. The following lines of evidence available from Bernard (1975) and Bernard and MacDonald (1974) and the results of this study support such a hypothesis. First, a substantial proportion of the population is in younger age classes at most times of the year. Many aquatic organisms have been shown to be more susceptible to heat stress during early developmental stages. Second annual population size in *C. lacustris* is dependent on shoot emergence the previous fall and the overwinter survival of this cohort. Thus, a high proportion of the population's biomass and carbohydrate reserve is above ground in winter where it is susceptible to exposure if increases in temperature or water flow rates prevent ice formation and snow cover or remove litter cover. Third, the life span of an individual shoot depends on time of emergence and fall height. If members of the fall cohort emerge early or grow too tall as a result of temperature changes they will not survive the winter. Fourth,

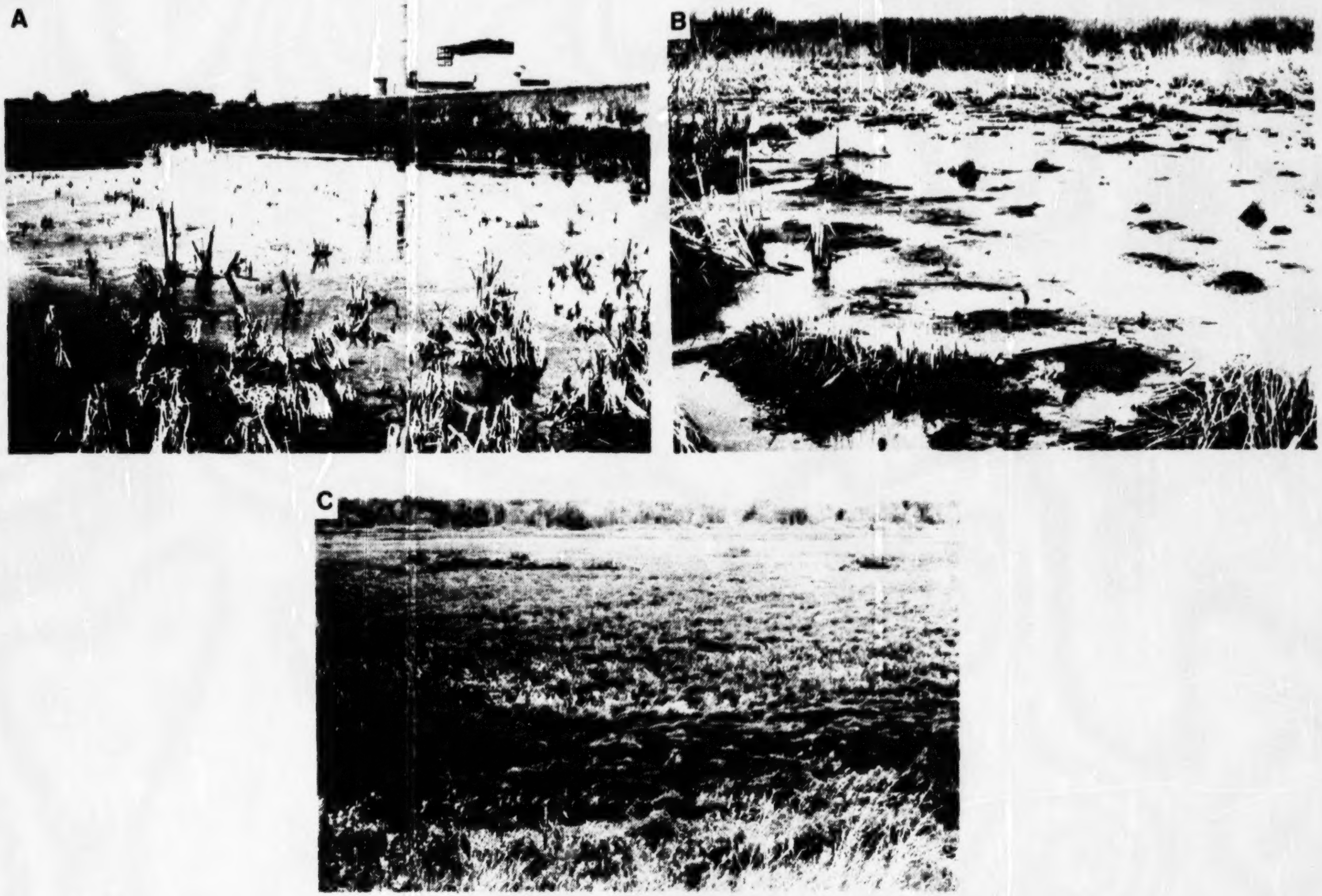

Figure 54. Areas of open water (A) and exposed mudflats (B) that have replaced the closed and densely vegetated perennial plant communities (C).

minor increases in temperature on the Columbia site altered the timing and growth of late summer- and fall-emerging shoots. The net effect of these characteristics appears to be population that is sensitive to heat stress throughout the year and is corroborated by the data. Unlike *T. latifolia, C. lacustris* showed visible signs of stress throughout the year. *C. rostrata*--a species with similar life history charactersitics (Bernard and MacDonald 1974, Bernard 1977, Bernard and Solsky 1978)--showed a similar response.

It is well known that plant species differ in their sensitivity to different kinds of disturbance. The results of this study suggest that species tolerance or senstivity is a consequence of the species life history cycle and the timing, as well as the magnitude of the disturbance. The charactersitic response to disturbance and the associated population consequences of three broad life history "stragegies" (syndromes) have been outlined by Grime (1977). Leith (1970), Bliss (1967), and Bernard and Gorham (1978) have pointed out the importance of phenological characteristics in determining species and community productivity. Erhlich and Holm (1962) suggested that species be grouped according to their ecological requirements. Animal (Stearns 1977) and terrestrial plant ecologists (Harper 1977) have conducted considerable research on life history characteristics in equilibrium communities. Environmental biologists should examine the concept of life history as a theoretical tool for predicting species sensitivity to disturbance and assessing the probable effects on wetland plant communities.

Previous studies (Harper 1969, Lubchenco 1978) and the population and community data from section 3 indicate that exogenous disturbance affects the process of vegetation change at the community level through the differential sensitivity of the dominant species. The results of this study suggest the importance of phenology in species response. The likelihood of predicting the response of dominant species would be enhanced by knowing the key charactersitics of its life cycle. These should include life span, the schedule of various phenophases, seasonal distribution of biomass between above- and below-ground parts, ability to regenerate or colonize, and reproduction and mortality schedules. Grouping species with similar sets of life history traits, especially temporal charactersitics, may identify meaningful aggregate variables (Orians 1980) for environmental impact assessment between the level of the individual species and the community.

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APPENDIX A

PLANT COMMUNITY DATA

Symbols used are defined as follows:

$\bar{S}$ is mean number of species per quadrat.

S is total number of species for all quadrats sampled:

$\bar{S}$ and S are measures of species richness

$$H' = -\sum_{i=1}^{n} p_i \ln p_i \qquad (1)$$

where

H' is the Shannon-Wiener diversity index (Peet 1975) combining species richness and the distribution of abundances of individuals in the different species, and

p_i is the proportion of total number of individuals contributed by species i

$$J = \frac{H'}{H'_{max}} = \frac{H'}{\ln S} \qquad (2)$$

where

J is the distribution of abundances in terms of their evenness or equitability and is the opposite of dominance, if J is low, dominance is high, and

H'_{max} is the maximum value of H' for the given number of species (S) (Pielou 1975).

TABLE A-1. SUMMER DATA FOR FOUR PLANT COMMUNITIES BEFORE (1974) AND FOLLOWING DISTURBANCE (1975 TO 1977) FOR AREA OF MAJOR IMPACT

Sampling	Community data including standard deviation			
period	$\bar{S}$	S	H'	J
		CAREX LACUSTRIS COMMUNITY		
1974	5.88 ± 2.06	26.00 ± 0.00	2.36 ± 0.00	0.72 ± 0.00
1975	4.08 ± 1.20	18.40 ± 0.55	1.68 ± 0.01	0.58 ± 0.00
1976	4.96 ± 2.08	22.80 ± 2.86	1.70 ± 0.20	0.54 ± 0.00
1977	7.46 ± 3.82	31.00 ± 3.39	2.18 ± 0.08	0.63 ± 0.00
1974 to 1977†	+1.58	+5.00	-0.18	-0.09
		CAREX STRICTA COMMUNITY		
1974	5.00 ± 1.16	19.00 ± 0.00	2.20 ± 0.00	0.75 ± 0.00
1975	4.75 ± 2.26	18.00 ± 0.00	1.43 ± 0.00	0.49 ± 0.00
1976	5.83 ± 3.02	18.80 ± 2.59	1.61 ± 0.08	0.55 ± 0.01
1977	7.06 ± 1.98	21.60 ± 2.88	1.84 ± 0.16	0.60 ± 0.06
1974 to 1977†	+2.06	+2.60	-0.36	-0.15
		EMERGENT COMMUNITY		
1974	3.38 ± 1.50	18.20 ± 1.10	1.87 ± 0.09	0.64 ± 0.02
1975	4.12 ± 1.36	11.00 ± 0.00	0.89 ± 0.00	0.37 ± 0.00
1976	3.38 ± 1.20	12.60 ± 2.07	0.80 ± 0.08	0.32 ± 0.03
1977	4.38 ± 1.97	14.00 ± 1.22	0.77 ± 0.08	0.29 ± 0.02
1974 to 1977†	+1.00	-4.20	-1.10	-0.35
		TRANSITION COMMUNITY		
1974	5.40 ± 2.22	15.00 ± 0.00	2.06 ± 0.00	0.76 ± 0.00
1975	4.05 ± 1.57	12.80 ± 2.59	1.62 ± 0.16	0.64 ± 0.05
1976	4.20 ± 1.00	11.20 ± 0.84	1.04 ± 0.10	0.43 ± 0.04
1977	5.09 ± 2.20	18.80 ± 2.28	1.38 ± 0.12	0.47 ± 0.03
1974 to 1977†	-0.31	+3.80	-0.68	-0.29

†Net change.

TABLE A-2. FALL DATA FOR FOUR PLANT COMMUNITIES BEFORE (1974) AND FOLLOWING DISTURBANCE (1975 TO 1977) FOR AREA OF MAJOR IMPACT

Sampling period	Community data including standard deviation			
	$\bar{S}$	S	H'	J
		CAREX LACUSTRIS COMMUNITY		
1974	4.10 ± 2.02	21.00 ± 0.00	1.90 ± 0.00	0.62 ± 0.00
1975	4.86 ± 1.56	16.80 ± 0.45	1.51 ± 0.23	0.51 ± 0.04
1976	3.96 ± 1.70	15.40 ± 2.30	1.46 ± 0.12	0.53 ± 0.04
1977	4.14 ± 2.05	19.80 ± 2.39	1.57 ± 0.16	0.53 ± 0.04
1974 to 1977†	+0.04	-1.20	-0.33	-0.09
		CAREX STRICTA COMMUNITY		
1974	4.90 ± 1.66	16.00 ± 0.00	1.60 ± 0.00	0.58 ± 0.00
1975	4.88 ± 2.45	16.60 ± 1.52	1.67 ± 0.06	0.60 ± 0.02
1976	4.00 ± 2.09	13.40 ± 3.78	1.25 ± 0.07	0.49 ± 0.05
1977	4.06 ± 2.07	11.60 ± 1.82	1.15 ± 0.08	0.47 ± 0.02
1974 to 1977†	-0.84	-4.40	-0.45	-0.11
		EMERGENT COMMUNITY		
1974	5.20 ± 1.81	19.00 ± 0.00	1.74 ± 0.00	0.66 ± 0.00
1975	4.15 ± 1.35	14.40 ± 0.55	1.29 ± 0.06	0.48 ± 0.02
1976	3.19 ± 1.13	9.00 ± 1.58	0.74 ± 0.13	0.34 ± 0.04
1977	3.17 ± 1.90	5.20 ± 1.30	0.41 ± 0.05	0.26 ± 0.06
1974 to 1977†	-2.03	-13.80	-1.53	-0.40
		TRANSITION COMMUNITY		
1974	5.00 ± 2.11	12.00 ± 0.00	1.70 ± 0.00	0.68 ± 0.00
1975	4.64 ± 1.33	11.00 ± 0.00	1.65 ± 0.00	0.69 ± 0.00
1976	4.09 ± 1.51	8.60 ± 1.14	1.15 ± 0.09	0.51 ± 0.08
1977	3.10 ± 1.10	10.80 ± 1.92	0.69 ± 0.15	0.29 ± 0.05
1974 to 1977†	-1.90	-1.20	-1.01	-0.39

†Net change.

TABLE A-3. SUMMER DATA FOR FIVE PLANT COMMUNITIES BEFORE (1974) AND FOLLOWING DISTURBANCE (1975 TO 1977) FOR ENTIRE AREA

Sampling period	Community data including standard deviation			
	$\bar{S}$	S	H'	J
		CAREX LACUSTRIS COMMUNITY		
1974	5.40 ± 1.93	41.00 ± 0.00	2.57 ± 0.00	0.69 ± 0.00
1975	4.20 ± 1.51	29.20 ± 1.64	2.18 ± 0.05	0.65 ± 0.01
		CAREX STRICTA COMMUNITY		
1974	5.60 ± 1.74	46.00 ± 0.00	2.66 ± 0.00	0.69 ± 0.00
1975	4.50 ± 1.71	42.80 ± 1.79	2.22 ± 0.03	0.59 ± 0.01
		EMERGENT COMMUNITY		
1974	3.90 ± 1.49	31.20 ± 0.80	2.23 ± 0.03	0.65 ± 0.01
1975	3.60 ± 1.11	16.00 ± 0.00	1.12 ± 0.00	0.40 ± 0.00
		TRANSITION COMMUNITY		
1974	5.30 ± 1.89	26.00 ± 0.00	2.55 ± 0.00	0.78 ± 0.00
1975	3.90 ± 1.40	19.20 ± 2.77	1.91 ± 0.13	0.65 ± 0.02
		SPIRAEA COMMUNITY		
1974	6.10 ± 2.28	30.00 ± 0.00	2.53 ± 0.00	0.74 ± 0.00
1975	4.60 ± 1.63	20.80 ± 0.84	1.97 ± 0.06	0.65 ± 0.00

†Net change.

TABLE A-4. FALL DATA FOR SIX PLANT COMMUNITIES BEFORE (1974) AND FOLLOWING DISTURBANCE (1975 TO 1977) FOR ENTIRE AREA

Sampling	Community data including standard deviation			
period	$\bar{S}$	S	H'	J
	CAREX LACUSTRIS COMMUNITY			
1974	5.27 ± 2.01	34.00 ± 0.00	1.44 ± 0.00	0.41 ± 0.00
1975	5.14 ± 2.14	30.20 ± 3.11	1.95 ± 0.12	0.57 ± 0.02
1976	3.88 ± 1.31	28.20 ± 1.92	1.72 ± 0.06	0.51 ± 0.02
1977	4.52 ± 2.08	30.00 ± 1.58	1.66 ± 0.10	0.49 ± 0.02
1974 to 1977†	-0.75	-4.00	+0.22	+0.08
	CAREX STRICTA COMMUNITY			
1974	5.22 ± 1.85	38.00 ± 0.00	1.83 ± 0.00	0.50 ± 0.00
1975	4.72 ± 2.06	46.40 ± 5.94	1.92 ± 0.12	0.51 ± 0.02
1976	3.77 ± 1.47	28.20 ± 1.30	1.68 ± 0.04	0.50 ± 0.01
1977	3.87 ± 1.58	34.00 ± 2.74	1.50 ± 0.09	0.42 ± 0.02
1974 to 1977†	-1.35	-4.00	-0.33	-0.08
	EMERGENT COMMUNITY			
1974	4.84 ± 1.50	30.00 ± 0.00	2.03 ± 0.00	0.60 ± 0.00
1975	3.95 ± 1.24	21.40 ± 1.95	1.49 ± 0.07	0.49 ± 0.02
1976	3.24 ± 1.16	14.40 ± 0.55	1.27 ± 0.05	0.48 ± 0.02
1977	2.94 ± 1.32	14.20 ± 1.10	0.74 ± 0.07	0.28 ± 0.03
1974 to 1977†	-1.90	-15.80	-1.29	-0.32
	TRANSITION COMMUNITY			
1974	5.38 ± 1.92	18.00 ± 0.00	1.97 ± 0.00	0.68 ± 0.00
1975	4.89 ± 2.23	21.60 ± 0.55	1.88 ± 0.04	0.61 ± 0.02
1976	3.76 ± 1.45	16.00 ± 1.73	1.31 ± 0.04	0.47 ± 0.02
1977	3.51 ± 1.58	31.60 ± 1.67	1.29 ± 0.16	0.37 ± 0.05
1974 to 1977†	-1.87	+13.60	-0.68	-0.31
	SPIRAEA COMMUNITY			
1974	5.12 ± 2.36	28.00 ± 0.00	2.30 ± 0.00	0.69 ± 0.00
1975	4.04 ± 1.91	20.60 ± 1.52	1.99 ± 0.02	0.66 ± 0.01
1976	4.58 ± 1.68	25.60 ± 1.67	1.72 ± 0.04	0.53 ± 0.02
1977	5.00 ± 1.86	24.40 ± 2.07	1.76 ± 0.09	0.55 ± 0.03
1974 to 1977†	-0.12	-3.60	-0.54	-0.14
	LOWLAND SHRUBS AND TREES			
1974	5.44 ± 1.67	37.00 ± 0.00	2.12 ± 0.00	0.59 ± 0.00
1975	4.35 ± 1.62	41.40 ± 3.36	1.94 ± 0.20	0.52 ± 0.05
1976	3.93 ± 1.46	28.20 ± 0.84	1.84 ± 0.07	0.55 ± 0.02
1977	3.84 ± 1.69	32.40 ± 3.78	1.73 ± 0.21	0.50 ± 0.04
1974 to 1977†	-1.60	-4.60	-0.39	-0.09

†Net change.

APPENDIX B

TOTAL NONSTRUCTURAL CARBOHYDRATE CONTENT OF *TYPHA LATIFOLIA* AND *CAREX LACUSTRIS*

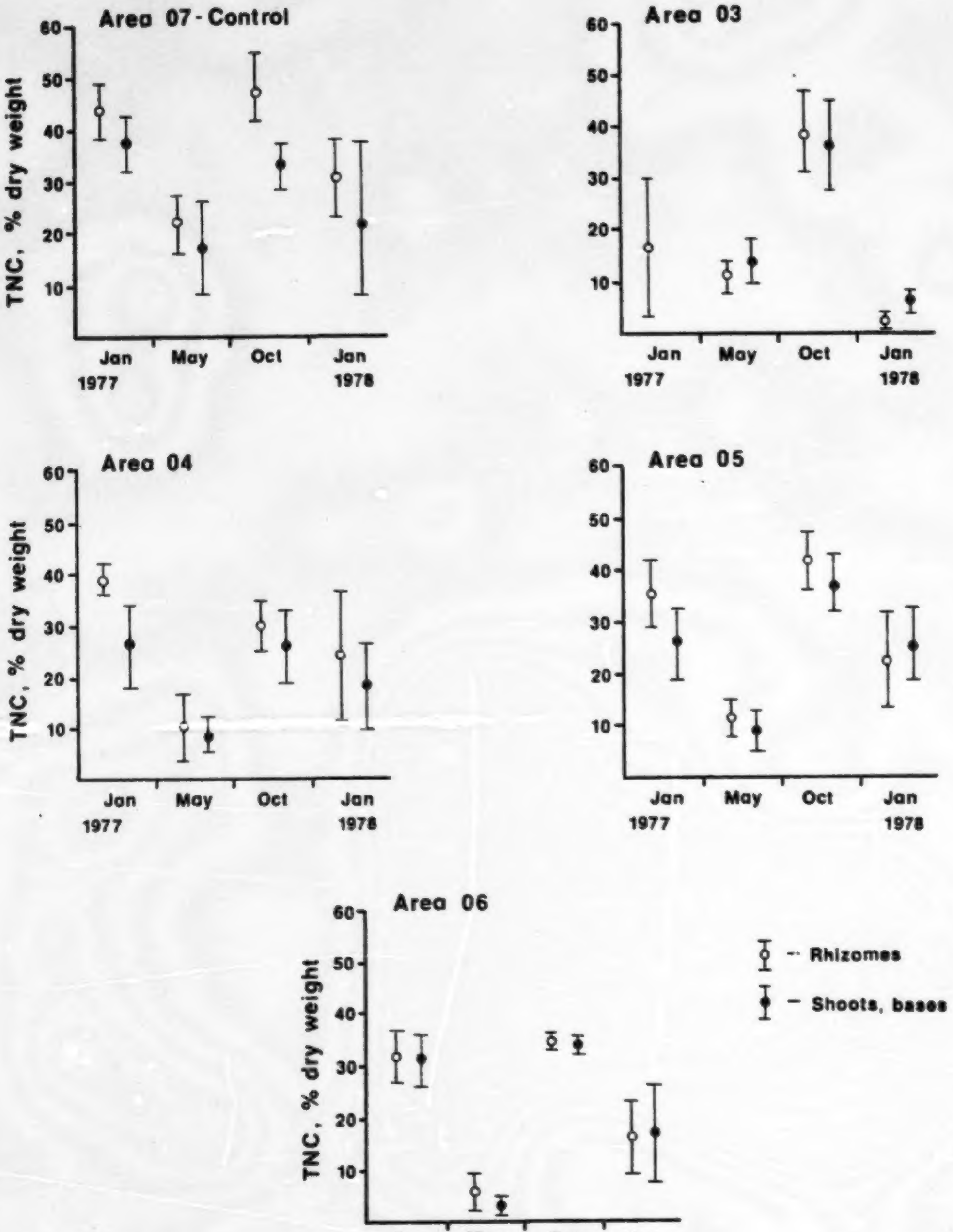

Figure B-1. Total nonstructural carbohydrates (%TNC ± s.d.) in rhizomes, shoots, and shoot bases of *Typha latifolia* at control (Area 07) and four other sites.

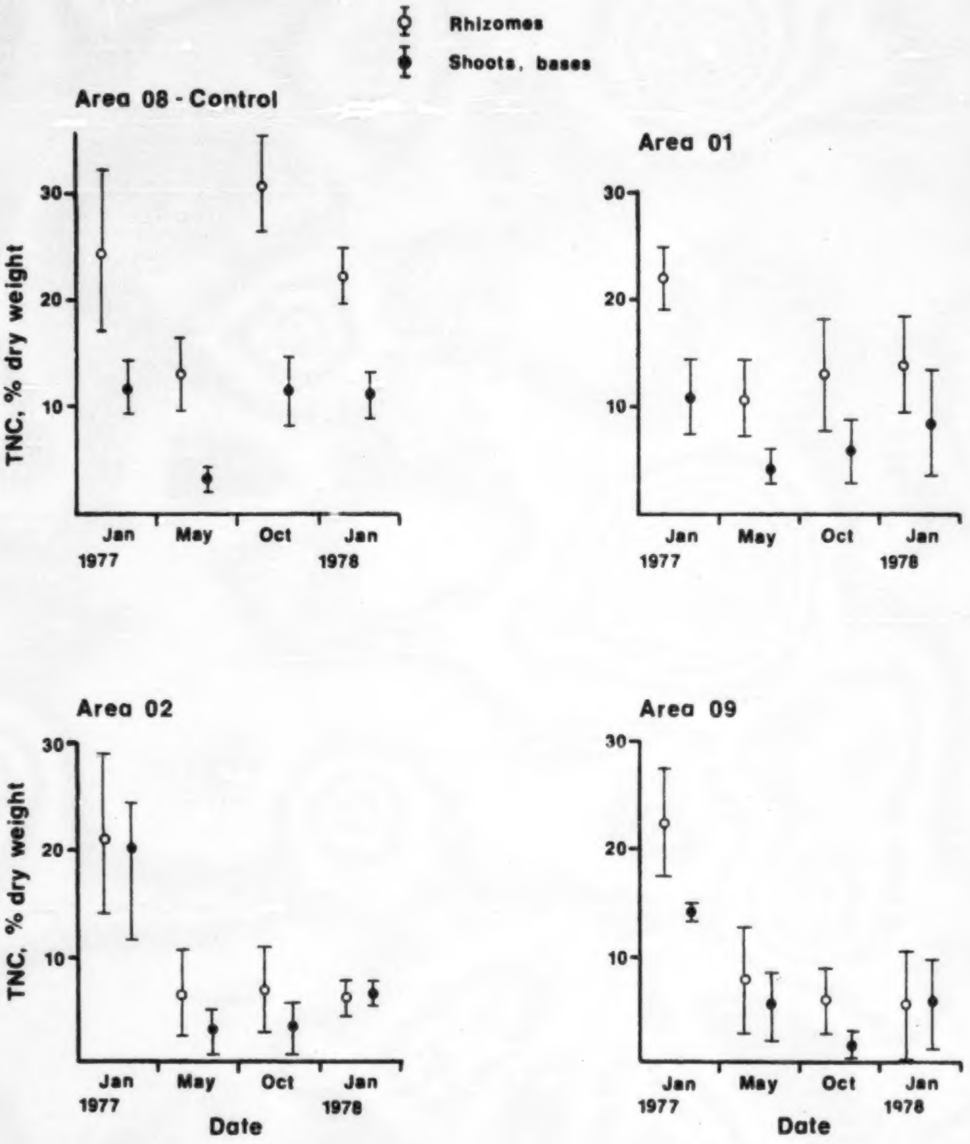

Figure B-2. Means and standard deviations for percent total nonstructural carbohydrates in rhizomes and shoot bases of *Carex lacustris* at three sites and a control (Area 08).